SILURIAN BRACHIOPODS OF THE SUPERFAMILY PLECTAMBONITACEA

BY
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Pp. 139–203 ; 17 *Plates* ; 9 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 19 No. 4
LONDON 1970

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 19, *No.* 4 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Geol.).

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 3 *November*, 1970 *Price* £5·10

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SYNOPSIS

Silurian plectambonitacean brachiopods are reviewed, and the number of British species reduced from twenty-three to eleven. Swedish and Bohemian forms are also considered, and the much quoted species *Eoplectodonta transversalis* (Wahlenberg 1819) and *Leangella segmentum* [Angelin MS] (Lindström 1861) are revised ; it is found that *E. transversalis* is confined to the Lower Visby Marl (uppermost Llandovery) of Gotland, and that the common Wenlock species of Britain and Sweden is *E. duvalii* (Davidson 1847). Most Silurian plectambonitaceans are extremely variable in shape and size.

The morphology and function of *Eoplectodonta* and *Leangella* are discussed, and the articulation and muscle systems described. It is postulated that when *Eoplectodonta* was being overturned, it could flap its valves, sending out water jets enabling it to right itself. It may also have achieved its water circulation by opening and closing its valves, a more efficient method than a ciliary beat in such a thin inter-valve space. The ecology is also considered, *Eoplectodonta*, *Ygerodiscus* and *Leangella* lived concave upwards free on the sea floor ; *Aegiria* lived an attached life, probably to algae. All the Silurian genera of the Plectambonitacea are most common in the deeper-water *Clorinda* Community.

I. INTRODUCTION

THIS paper continues the study of Silurian strophomenide brachiopods. The scope has widened ; the first paper, on the strophеodontids (Cocks 1967), dealt only with the Llandovery of the Welsh Borderland, the second, on the strophomenids (Cocks 1968), covered the Llandovery of Britain. The present paper includes at least a review of all the species so far described from the Silurian of Europe.

One of the reasons for the increase in age range is that the plectambonitaceans found in the Upper Silurian, i.e. the Wenlock and Ludlow Series, are on the whole lingering members of genera common in the Llandovery. Indeed, after the appearance of *Ygerodiscus* at the end of the Lower Llandovery, no new genera of plectambonitaceans appeared in Europe until the very close of the Silurian.

The acme of the Plectambonitacea was in the Middle Ordovician, after an explosive radiation in the upper part of the Lower Ordovician. Of the six families and twelve subfamilies in the Treatise on Invertebrate Paleontology (Williams 1965), whose classification is followed here, only two families and four subfamilies have representatives in the Silurian, although individual species may be very abundant. Their ecological niches were occupied first by small strophеodontids, such as *Pholidostrophia* and then later by the chonetids, and the whole of the superfamily Plectambonitacea was extinct by the beginning of the Upper Devonian.

No-one appears to have appreciated the extreme variability of Silurian plectambonitaceans in exterior shell proportions and in the varied development of internal structures, both as adults and during ontogeny. A large number of names have been erected in the past for forms within the limits of each other's variability ; hence the many taxa put into synonomy in this paper. No new species or genera have been erected.

The Plectambonitacea possess a very different morphology from any living brachiopod, and their possible mode of life is discussed.

New stages have recently been erected within the Llandovery Series (Cocks, Toghill & Ziegler, 1970), in ascending order Rhuddanian, Idwian, Fronian and Telychian, and these names are used in this paper.

II. HISTORY OF PREVIOUS RESEARCH

During the nineteenth century, Silurian species of plectambonitaceans were described by J. de C. Sowerby, Davidson and Salter in Britain, and by Wahlenberg, Shaler, Barrande and Lindström abroad. Most were allotted to the genus *Leptaena*, to which Dalman (1828) had referred the first described species, Wahlenberg's *Anomites transversalis*. Not until a paper by Reed appeared in 1917 were satisfactory descriptions published ; however his work was confined to the Girvan district of Scotland.

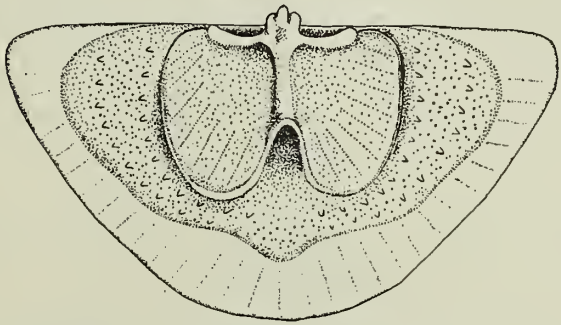

FIG. 1. Brachial valve of *Leangella scissa*.

The only major paper on British Silurian plectambonitaceans is that by O. T. Jones (1928), whose interest in the group was aroused at the turn of the century when working for the Geological Survey. In Pembrokeshire and Carmarthenshire the Ordovician and Silurian rocks consist mainly of rather similar mudstones, and Jones recognised a succession of plectambonitacean faunas in the Llandeilo, Bala and Llandovery rocks, which he was able to use in mapping (Jones *in* Strahan *et al.* 1914 ; Cantrill *et al.* 1916).

Subsequently (1928), he described three new genera of plectambonitaceans, *Sowerbyella*, *Leptelloidea* and *Chonetoidea*, with twelve new species and six new " varieties " of which seven species and four " varieties " are from the Lower Silurian, chiefly of Pembrokeshire.

There followed Kozlowski's great work (1929) on the Silurian (now mostly Lower Devonian) of Podolia, then in Poland, now in Russia. He separated those sowerbyellids with denticles into a new genus, *Plectodonta* ; and, as its inferred predecessor, the partly denticulate sub-genus *Eoplectodonta* (with as type one of Jones's Welsh species, *Sowerbyella precursor*). Soon afterwards, Öpik, working on Baltic material (1932, 1933), clarified the familial divisions within the plectambonitaceans, and, although dealing mainly with Ordovician forms, divided Jones's genus *Chonetoidea* into *Chonetoidea* and *Aegiria*, and *Leptelloidea* into *Leptelloidea* and *Leangella*. Öpik's elucidation of plectambonitacean morphology represented a great advance.

Since then there has been no published work on British Silurian species, apart from a paper by Lamont & Gilbert (1945) in which the rare genus *Merciella* was named. Abroad, a few species have been described, as an incidental part of larger faunal

studies, but the only major contributor has been Havlíček (1952, 1961, 1967) with detailed studies on the Bohemian fauna. However much knowledge has been gained on Ordovician forms, particularly by Cooper (1956) and Williams (1962 etc.), and an acceptable classification has been formulated (Williams 1965).

III. MORPHOLOGICAL TERMINOLOGY

In most descriptions of the superfamily, the morphological terminology used has been based on the assumed function of the structures, although the Plectambonitacea are among those brachiopods in which direct homology with living forms is most conjectural. Thus a descriptive terminology is defined and used in this paper without functional connotation ; the attempt is made subsequently to assess the use of the structures in the live animal. There is a shortage of terms which do not connote some degree of function, and it has been necessary to create two new terms, bema and clavicular plates.

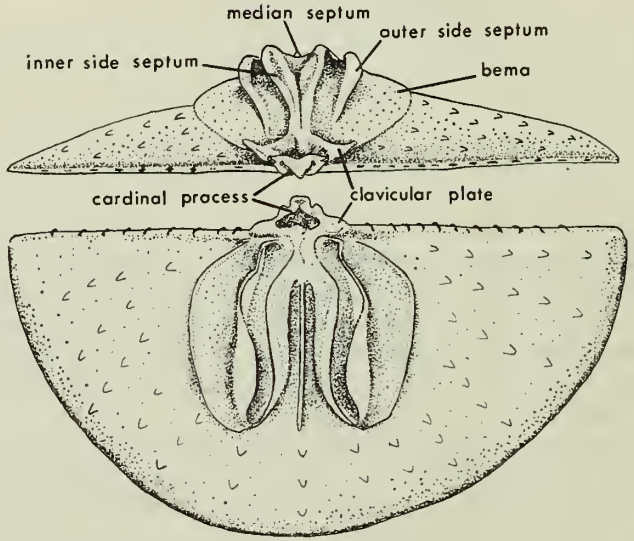

Fig. 2. Brachial valve of *Eoplectodonta duvalii*.

The term " anderidium " (Sadlick 1965) was defined primarily for the chonetids (according to its original definition it replaces the term " lateral septa " as used by Muir-Wood, 1962, fig. 3A). Sadlick refers to the " anderidia " of sowerbyellids, but he does not elaborate on this use, or provide or refer to illustrations. Thus it is not clear which structures he had in mind for sowerbyellids, and whether these would be homologous with the anderidia in chonetids, and so the term is not used in this paper.

Gill (1969), whilst describing the Notanopliidae, an interesting Devonian group which might have been descended from some sowerbyellid, erected a new series of names for various sets of septa in both valves. He rightly draws distinctions be-

tween the different functions of the sets of septa, but he draws these distinctions before giving them their names. If the organ were to be interpreted differently by any subsequent worker, then the name would need changing, i.e. it is again a subjective system, and has not been used in this paper. Gill also restricts the use of the terms ventral median septum (which he calls " venmidseptum ") and dorsal median septum (which he calls " dormidseptum ") to structures which commence at the hinge line. Since the meaning of septum is " something which encloses something " (and has been used in brachiopod morphology for many years as meaning some sort of small wall, usually radial, inside any part of a brachiopod valve), and " median " is also unambiguous, it seems a pity to restrict the meaning of this useful term to structures which reach the hinge line ; for this reason Gill's restriction of the terms is not followed.

Another feature often seen inside plectambonitacean brachial valves is a depression bounded posteriorly by the cardinal process, postero-laterally by the socket plates and anteriorly by the median high septal field. Some authors have named this depression ; Öpik (1933) called it the " Schlossgrube " and Muir-Wood (1962) the " alveolus ". However it can be misleading to use positive terms for negative features, and I prefer to think of this space as a gap between structures, rather than as a structure in its own right, and so a special name is not used in this paper.

There follows a glossary of some of the morphological terms used in this paper for the two families, together with the equivalents of previous workers (Jones 1928, Kozlowski 1929, Öpik 1933, Williams 1965 and Havlíček 1967). Other terms used will be found in the Treatise on Invertebrate Paleontology (Williams *et al.* 1965).

LEPTELLINIDAE

Central shaft and **lateral processes** of cardinal process : the cardinal process is trifid, with a central shaft and two, or sometimes four, lateral processes (Jones : cardinal process, Öpik : Mittelzapfen des Schlossfortzatzes und seitlichen Zapfens, Williams : cardinal process and subsidiary ridges).

Dental Plates : pair of structures supporting the teeth, between them and the floor of the pedicle valve (Jones : dental lamallae, Williams : dental plates).

Platform : raised area of secondary shell in the brachial valve upon which striae are often seen (Jones : visceral disc, Öpik : Brachiallamellen, Williams : lophophore platform, Havlíček : visceral platform).

Socket Plates : pair of structures forming the anterior support in the brachial valve for the pedicle valve teeth (Jones : crural bases, Williams : socket ridges, Havlíček : brachiophores).

Subperipheral rim : ridge running round either valve subparallel with the anterior commisure which curves round posteriorly to merge with the hinge line or the bases of the socket plates (Jones : concentric elevation, Öpik : Diaphragma (in brachial valve), Akkomodationspur des Diaphragmas (in pedicle valve), Williams : subperipheral rim, Havlíček : diaphragm (in brachial valve), submarginal ridge (in pedicle valve)).

SOWERBYELLIDAE

Bema (new term, from Greek βῆμα meaning a platform) : platform of secondary shell in the central field of the brachial valve, its function is discussed below. A new term is coined since it is debateable whether this organ is homologous with the platform of the Leptellinidae. It is certainly different in structure, hence a new objective term with no functional connotation (Kozlowski : branche externe de la lamelle brachiale, Öpik : Brachiallamellen, Williams : lophophore platform, Havlíček : peripheral rim of visceral field).

Clavicular plates (new term from Latin *clavis*, meaning a key) : pair of structures projecting antero-laterally from the cardinal process ; their function is discussed below (Kozlowski : plaques crurales, Öpik : Cruralzähnen, Williams : socket ridges).

Fossettes : a series of small pits along the hinge line into which the denticles of the opposite valve fit (Kozlowski : fossettes denticulaires).

Inner side septa : the pair of septa in the brachial valve which lie immediately laterally of the median septum (Jones : submedian septa, Kozlowski : branche interne de la lamelle brachiale, Öpik : Seitensepten, Williams : submedian septa).

Outer side septa : the pair of septa in the brachial valve which lie outside the inner side septa (Jones : transverse septa, Kozlowski : lamelle brachiale intralobaire, Öpik : Seitensepten, Williams : divergent ridges).

IV. FUNCTIONAL MORPHOLOGY

No living brachiopod has a form similar to the Plectambonitacea. The extreme thinness of a plectambonitacean (when its valves were together) in relation to its valve area, and in addition its curved shape, often more than a semicircle in cross-section, make comparison with living brachiopods impossible in all but the most general way ; the terebratulides, rhynchonellides and thecideaceans all have a relatively large internal cavity in proportion to their valve size.

In this section attention will be confined to the two most common Silurian plectambonitacean genera, *Leangella* and *Eoplectodonta*. The other genera described in this paper are presumed to have functioned in a similar way to these two genera, except *Chonetoidea* and its close relative *Aegiria*, which differ in having a functional pedicle.

The articulation system, the muscle system, the water circulation-feeding system and the mantle canal system will be considered in turn.

Articulation.

The Ordovician *Sowerbyella* had a simple articulation consisting of a pair of teeth in the pedicle valve which fitted into the brachial valve between the hinge line and a pair of socket plates (both well figured in *Sowerbyella nasuta* by Cooper, 1956, pl. 199). Both these structures occur in the earliest, Middle Ordovician, species of *Eoplectodonta* in which Cooper described small teeth as well as socket plates (1956 : 808, also pl. 208). They also possess denticles on the pedicle valve hinge line with corresponding fossettes in the brachial valve, one of the primary diagnostic features of *Eoplectodonta*.

Incidentally there is no correlation between the proportion of the hinge line covered by denticles and the geological age of the species, as supposed by Kozlowski (1929) when he erected *Eoplectodonta*. Smaller teeth are still present in some Ashgill species. However by early Silurian time none of the species of *Eoplectodonta* had teeth ; presumably articulation was achieved by the system of denticles and fossettes on the hinge line. However they all possessed well developed " socket plates " in the brachial valve. Since these " socket plates " could not have performed their named function in those Silurian species without teeth, the term " clavicular plates " has

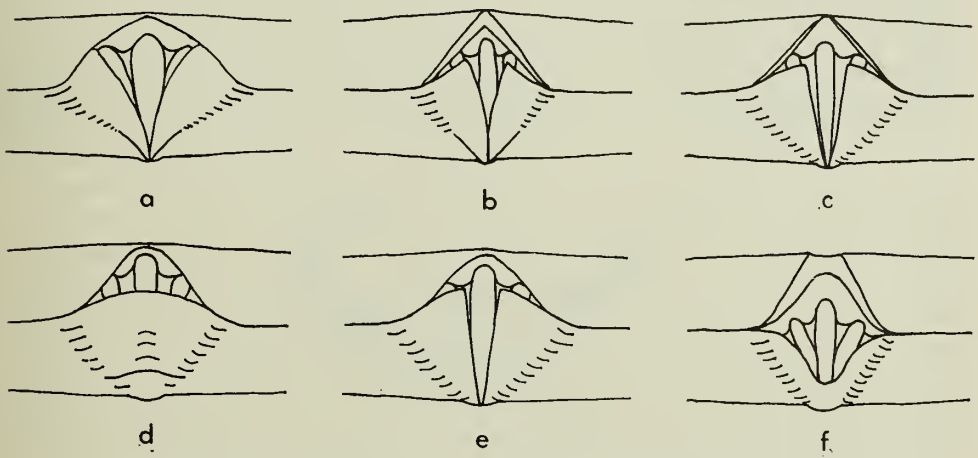

FIG. 3. Interareas of *Eoplectodonta* (a–e) and *Plectodonta* (f), pedicle valve above, brachial valve below. (a) *E. duplicata* (from BB 31738, Lower Llandovery, Gasworks Mudstone, Wales) with open delthyrium and chilidial plates, behind them the central shaft and lateral processes of the cardinal process. (b) *E. penkillensis* (from BB 31840, Upper Llandovery, Hughley Shales, England) showing blade-like deltidial plates and chilidial plates. (c) *E. transversalis* (from BB 32422 Upper Llandovery, Lower Visby Marl, Sweden) showing chilidial plates and very small deltidial plates. (d) and (e) *E. duvalii* from the same locality (both registered B 1587 from Lower Wenlock, Buildwas Beds, England) both with open delthyrium, but one specimen with entire chilidium and the other with discrete pair of chilidial plates. (f) *Plectodonta mariae* (from B 81377, Lower Devonian, Borschov Beds, U.S.S.R.) showing deltidium and low but entire chilidium. What these diagrams do not convey is the relative angles of the interareas of the two valves, which are sometimes great, for example in *E. duvalii* ; however the interareas of *P. mariae* are set in nearly the same plane.

been used in this paper for these structures. These clavicular plates grew in the same way as the socket plates of the Ordovician species with teeth, but the fact of their continued existence after the teeth had vanished from the stock, argues that the clavicular plates must have had some function in addition to their now obsolete role as socket plates. Havlíček, without discussion, describes the clavicular plates as brachiophores. However there is no direct evidence for this function, which is why an objective term has been coined here for the plates. It is possible that they might

have functioned as brachiophores, giving some sort of rigid support to the ends of the lophophores ; on the other hand they may simply have given some support to some organ within the coelome.

In contrast, the teeth and socket plates of *Leangella* remained until its extinction.

The muscle system.

The diductor muscle system of *Eoplectodonta* consisted of a pair of muscles running from the small scars on each side of the short median septum in the umbo of the pedicle valve to the pair of furrows at the top of the prominent cardinal process. The adductor muscle system is open to more varied interpretation. In the pedicle valve there is a very large pair of diamond-shaped scars in the umbonal region (Plate 6, figs. 1, 2, 7–9), but in the brachial valve there is no obvious site for muscle attachment (Plate 5, figs. 3–12). The oval areas to be seen on the specimens figured on Plate 5, figs. 3 and 6 and Plate 6, figs. 4 and 5, in the antero-median area of the brachial valves, are present between the median septa and inner side septa in only a very few valves from the Gasworks Mudstone, and may represent areas from which mantle tissue had been worn during adult life by contact with the pedicle valve when the valves were shut. In any case, the fact that these areas are absent from nearly all brachial valves precludes their choice as a probable attachment site for the adductor scars. The adductor muscles were probably attached in the brachial valve to the outer sides of the outer side septa and onto the bema, between its lateral edges and the outer side septa, since they are opposite the scars in the pedicle valve. Considering the antero-lateral splaying of the pedicle valve adductor scars and the shape of both valves, that general area of the brachial valve would be the most likely place for the attachment of the adductor muscles on mechanical grounds.

In *Leangella* the system is more certain. The diductor muscles went from the small lanceolate scars in the pedicle valve umbo to the cardinal process, in a similar way to *Eoplectodonta*. The adductor muscles ran from the umbonal muscle field in the pedicle valve, which was raised up off the valve floor to form a platform, to the muscle platform in the brachial valve. On both valves the attachment striae are clearly visible (Plate 1, fig. 12 for pedicle valve and Plate 4, figs. 9 and 10 for the brachial valve).

Thus in both *Eoplectodonta* and *Leangella* there was a notably strong muscle system. The reasons for this will now be considered.

As adduced in the section on ecology below, plectambonitaceans must have lived concave upwards. On the other hand, such a position is not as hydrodynamically stable as convex upwards, and when any sort of severe current or wave action occurred then the brachiopod would have been overturned and killed, particularly as its pedicle was apparently non-functional in adults. As a result, the Plectambonitacea may well have evolved to increase the strength of their muscle system so that individuals could right themselves by a series of snapping actions whilst they were in process of being overturned. *Eoplectodonta* also possesses a septal system which is tubular (in cross-section parallel to the hinge line). When the water was expelled quickly from inside the brachiopods by quick action of the adductor muscles, these tubes would have directed much of the water anteriorly in jets, a far more effective

righting mechanism than an indiscriminate expulsion of water equally round the gape. This power of self-righting would obviously have had a high survival advantage. How these brachiopods may have used this strong muscle system in a secondary role is discussed below.

Water Circulation and Feeding System.

All modern articulate brachiopods feed by creating a current of water from the beating of the cilia on their lophophores, and then by straining the food from the water as it swirls between the two valves. The straining is achieved by the separation of the space between the valves into two compartments, for water before and after it has been strained (Rudwick 1962). As a result, various fairly rigid lophophore systems, often with calcareous supports, have evolved, adapted to the dual function of creating a ciliary beat for water circulation and of straining the particles from the water and passing them to the mouth.

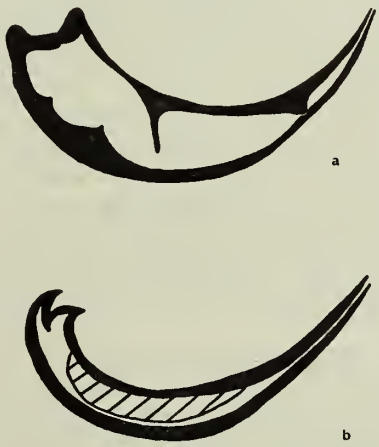

FIG. 4. Cross-section through the median plane of (a) *Leangella* and (b) *Eoplectodonta*. The shaded area in *Eoplectodonta* shows the profile of one of the inner side septa.

Eoplectodonta, and by inference other plectambonitaceans, may have accomplished the water circulation in a different way. As seen above, the animals had a powerful muscle system. The simple action of opening or closing their valves would have caused a very large increase in the volume of water inside the shell. An opening of about ten degrees would cause the shell to hold about four times as much water as when the valves were shut. As the valves opened, a large quantity of water would have come in, with the largest part of the volume in the central part of the shell, where the gape would be at its maximum. In cross-section parallel to the hinge line the spaces between the inner and outer septa are tubular anteriorly, and widen out again posteriorly. This arrangement would help to channel the incoming or outgoing water to make the system more controlled. Another feature which improved

the water circulation is the increased valve length. For about their anterior third, adult valves grew more or less parallel to each other (Text-fig. 4), so that when the valves were shut the whole of that sector of the valves were very close together, and that when the valves opened there would have been a faster and more forceful inrush of water than if the extra valve length had not been there. However, this latter advantage may have been partially offset by the increased weight of the added calcification, and the extra anterior valve length may simply have been to keep the commissural feeding gape higher off the substrate.

This system of water circulation would obviate the need for a ciliary beat circulation system, and the latter could even have atrophied, possibly in the stock as a whole some time during the Ordovician, or possibly in each individual soon after the larval stage. The lophophore would then be relegated into a role solely concerned with the collection of food. The septal tubes and general valve morphology would channel the water right up near the mouth of the animal, and the lophophore could either have degenerated into a small filtering device just round the mouth area, or it could have remained as a larger structure perhaps adhering to the septa or floor of the bema. On the other hand, a weak ciliary beat could have continued through life, so as to help control the filtering, and as a means of rejection of unwanted particles.

In *Leangella* a similar system might have operated. Here the subperipheral rim in the brachial valve and its interlocking counterpart in the pedicle valve (Text-fig. 4b) provides the narrow point through which the water would have rushed through quickly when the valves opened. In *L. scissa* (Plate 2, fig. 4) the anterior part of the subperipheral rim was curved in such a fashion as to direct the incoming or outgoing water centrally up the valve. In *Leangella*, as may be seen from the striae, the muscle system occupied all of the platform area, and the lophophore was presumably arranged in the area between the muscle platform and the subperipheral rim.

In both *Eoplectodonta* and *Leangella* the papillae are markedly coarser, but less numerous, in the brachial valve as opposed to the pedicle valve. It is possible that this arrangement provided a better attachment surface in the brachial valve for the mantle, since that valve would have been in motion for a much greater part of the time than the largely sessile pedicle valve.

No living brachiopod achieves its water circulation by the valve movement method postulated above. However the same idea has been put forward for another extinct group of strophomenides, the Richthofenacea. Rudwick (1961) has advanced the theory that these rather aberrant, coral-shaped brachiopods circulated their water by flapping their lid-like brachial valves ; but the morphology of the Richthofenacea is even further removed from that of a conventional brachiopod than that of the Plectambonitacea.

The Mantle Canal System.

There is some variation seen in the mantle canal patterns of the pedicle valve of *Eoplectodonta* (Text-fig. 5). The *vascula media* are prominent, although the *vascula genitalia* and gonadal sac area illustrated by Williams (1965 : H131) for *Sowerbyella* have not been seen.

In nearly all specimens of *Eoplectodonta* the mantle canals are well impressed in the pedicle valve, whilst in the brachial valve there is usually no trace of them, even allowing for the fact that the edge of the main body coelome would have come further anteriorly in the brachial valve than in the pedicle valve. A possible reason for this discrepancy (if it is real rather than apparent) follows from the interpretation of the muscle and water circulation systems discussed above. Since the anterior parts of the two valves were more or less parallel to each other (Text-fig. 4), the setae at the ends of the vascular system would also have been more or less parallel, assuming, that is, that the setal direction in plectambonitaceans was similar to that of modern brachiopods, in the same plane as valve growth (as illustrated by Williams 1965 : H82). If they were parallel, then the functions of the setae in the two valves

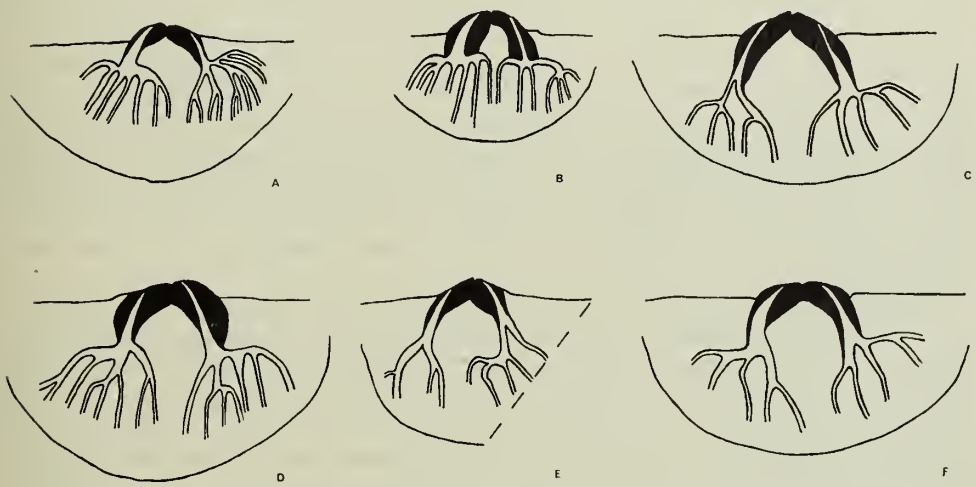

FIG. 5. Mantle canal patterns in the pedicle valve of *Eoplectodonta duplicata*. The figures are drawn as internal moulds and the adductor muscle scars coloured black. (a) from BB 31990 (Plate 8, figs. 3, 4), Woodland Point, Girvan, (b) from GSM 37579, Plate 8, fig. 7), Gasworks Sandstone, Union Hill, Pembrokeshire. (c) to (f) all from Gasworks Mudstone, the Gasworks, Haverfordwest, Pembrokeshire (c) BB 31753 (Plate 6, fig. 8), (d) and (e) both BB 31732 (Plate 6, fig. 3), (f) BB 31740 (Plate 6, fig. 7).

would have been to some degree duplicatory. Since the brachial valve would have been in motion much more than the pedicle valve, it would obviously have preferred to lighten its load as much as possible. For these reasons, the setae, and the corresponding mantle canals, could have become enlarged in the pedicle valve as compared with the brachial valve.

However there is no suggestion that the setae and vascular system became atrophied in the brachial valve ; there are rare specimens of *Eoplectodonta* (for example the individual figured in Plate 5, figs. 3 and 6) in which the mantle canal

system is clearly visible, starting as two trunks (presumably the *vascula myaria*) at the anterior end of the bema, and radiating in a manner similar to that of the pedicle valve.

V. ECOLOGY

The autecology of the animals will be considered first, followed by the synecology. *Leangella*, *Eoplectodonta* and *Ygerodiscus* (and also probably *Merciella* and *Anisopleurella*, but there is too little material to be sure) were presumably benthic forms. Their pedicles were wholly or partly atrophied during adult life, and they lay free on the sea floor. The only stable positions for shells of highly curved shape is with the diameter of the valve semicircle lying parallel with the sea bed. This gives a choice of two positions, with pedicle valve on top or with pedicle valve underneath. As argued by Williams (1953 : 33) for the stropheodontids, brachiopods derive their food from circulating sea water, and this could only have entered through the gap between the two valves. If the pedicle valve was uppermost, it follows that this gap would have been buried in the sea floor, an impossible condition for the circulation of water. Thus these genera must have lived with their pedicle valve downwards on the substrate, which they appear to have preferred to be soft. As argued in the section on functional morphology above, they probably also had the power to right themselves if tipped off balance, by a quick muscular snapping action. On death, however, they would have been easily upturned by currents into the hydrodynamically more stable position, i.e. pedicle valve on top, in which they are very often found fossil.

Havlíček (1967) and Bergström (1968) have demonstrated the case for an epiplanktonic existence for some plectambonitacean genera, in particular *Chonetoidea*. Both these authors figured strings of valves in apparent life association, and also associated, in Bergström's case, with dark, presumably organic, patches which may have been algal in origin. In the Silurian *Aegiria* is sometimes found in the same way occurring occasionally in rocks in which the other benthic fauna is restricted, suggesting adverse conditions. However *Aegiria* also occurs in ones and twos as an apparently normal constituent of the *Clorinda* Community. There is no appreciable difference in the morphology of *Aegiria* in these two forms of occurrence. All *Aegiria* have a foramen big enough to contain a pedicle which was presumably functional, and a possible way to reconcile the two types of occurrence is to postulate that *Aegiria* normally lived an attached life, perhaps to brown or red algae, at *Clorinda* Community depth. From time to time strands of algae were uprooted, and transported, together with the attached *Aegiria*, into environments which were inimical to brachiopods, at times even euxinic. The brachiopods attached to the algae thus drifted further than the other brachiopod genera which lay free on the sea floor. It is also possible that in the Silurian some species of the atrypoid *Glassia* lived in a similar manner to that of *Aegiria*.

As for the synecology, the animal communities (Ziegler, Cocks & Bambach, 1968) in which the British species of Plectambonitacea lived during the Llandovery may be listed as follows (no plectambonitaceans have been found in the shallowest water *Lingula* Community, which is omitted):

	Eocoelia Community	*Pentamerus* Community	*Stricklandia* Community	*Clorinda* Community
Merciella vesper Lamont & Gilbert	—	—	o	—
Leangella scissa (Davidson)	—	r	c	o
Leangella segmentum (Lindström)	—	—	r	c
Eoplectodonta duplicata (J. de C Sowerby)	o	(o)	D	D
Eoplectodonta penkillensis (Reed)	—	r	o	D
Eoplectodonta duvalii (Davidson)	—	r	o	D
Ygerodiscus undulatus (Salter)	—	r	c	c
Anisopleurella gracilis (Jones)	—	—	—	D
Aegiria grayi (Davidson)	—	—	r	c

The communities listed above apply to clastic rocks deposited in level bottom basins (the brackets round the *Pentamerus* Community occurrence signifies that that community cannot be separated from the *Stricklandia* Community in the Lower Llandovery where *P. duplicata* occurs). The dashes indicate non-occurrence, r means rare, o means that it occurs sporadically, c means that it is often common in the community, and D indicates that the species may sometimes be the most dominant form found in some developments of the community. Many plectambonitids occur in limestones, particularly of Wenlock age, and animal communities have not yet been defined in these ; one of the drawbacks being the possibility of an abundance of microenvironments amongst the patch reefs and other sea-floor carbonate facies. Complete information is not yet available on the community structure of the European Silurian or of the Wenlock and Ludlow in Britain. However it is probable that the associations found in the Lower Visby Marl of Gotland and the Wenlock Shale of the Welsh Borderland may be termed *Clorinda* Communities in the same sense as that used by Ziegler *et al.*, although all the constituents are not exactly the same.

The study of the synecology of *Eoplectodonta* is particularly interesting since it apparently underwent a radical change near the beginning of Silurian time. During the Ordovician, sowerbyellids seem to have been fairly shallow water forms (Bretsky 1969), perhaps in the ecological equivalent of the *Eocoelia* Community (Bretsky 1969a). The lower Llandovery equivalent of the *Eocoelia* Community is the *Cryptothyrella* Community, and in the lower Llandovery only, the Rhuddanian, *Eoplectodonta* is found in the *Cryptothyrella* Community, for example at Mulloch Hill, Girvan, Scotland. This is the type locality of *Eoplectodonta mullochensis* (Reed), considered in this paper to be a junior synonym of *E. duplicata* (J. de C. Sowerby). That the *Cryptothyrella* Community was genuinely shallow-water is supported by the common occurrence in it at Mulloch Hill of the dasycladacean alga *Mastopora fava* (Salter), which Dr. G. F. Elliott states would only be likely to grow in a water depth of from a few centimetres to a few metres. The age of this occurrence is pre-*cyphus*

Zone (from as yet unpublished work by the present author and Dr. P. Toghill). But at approximately the same time, only a few miles away at Woodland Point, Girvan, the same species was present in a *Stricklandia* Community, and by the end of Rhuddanian time *Eoplectodonta* is found in the *Clorinda* Community, sometimes even in dominating numbers, and not at all in the shallower-water communities. Throughout the rest of the Llandovery, at least in clastic rocks, *Eoplectodonta* is one of the most characteristic members of the deeper-water *Clorinda* Community, being quite uncommon in the neighbouring *Stricklandia* Community.

The ecological niche left by the migration of the sowerbyellids from the shallower communities seems at first to have been partly filled by pholidostrophiids, and then, towards the end of Silurian time, by a great increase in the abundance of chonetids, which are rare in the Llandovery.

VI. SYSTEMATIC PALAEONTOLOGY

Superfamily **PLECTAMBONITACEA** Jones 1928

Classification.

In the Treatise on Invertebrate Paleontology, Williams (1965) classified the Plectambonitacea as follows (only families and Silurian subfamilies mentioned here):

Family Plectambonitidae Jones 1928 (Lower to Middle Ord.)
Family Taffiidae Ulrich & Cooper 1936 (Lower Ord.)
Family Leptestiidae Öpik 1933 (Lower to Upper Ord.)
Family Leptellinidae Ulrich & Cooper 1936
  Subfamily Leptellininae Ulrich & Cooper 1936 (Lower Ord. to Lower Sil.)
  Subfamily Leptellinae Williams 1965 (Lower Ord.)
  Subfamily Leptestiinae Havlíček 1961 (Middle Ord. to Upper Sil.)
Family Sowerbyellidae Öpik 1930
  Subfamily Sowerbyellinae Öpik 1930 (Ord. to Middle Dev.)
  Subfamily Ptychoglyptinae Cooper 1956 (Ord.)
  Subfamily Xenambonitinae Cooper 1956 (Middle to Upper Ord.)
  Subfamily Aegiromeninae Havlíček 1961 (Middle Ord. to Lower Sil.)
Family Bimuriidae Cooper 1956 (Middle Ord.)

Havlíček's classification (1967) of the superfamily is similar except in the following respects :

(i) Following Rõõmusoks (1963) he uses the monotypic family Anoptambonitidae (Williams put *Anoptambonites* into the Leptellininae).

(ii) He creates the new family Dubioleptinidae, to include only one species, *Dubioleptina expulsa* (Barrande), of Wenlock age, which is distinctive in the " absence of brachiophores ".

I have only briefly seen material of *Dubioleptina expulsa*, but from Havlíček's excellent illustrations, I would class the genus with the Sowerbyellinae. The loss of the " brachiophores ", which I would term here clavicular plates, is only to be expected in advanced forms after the loss of the corresponding teeth in the pedicle valve.

Thus, apart from the Dubioleptinidae, the classifications of both Williams and

Havlíček are the same for Silurian forms, and nothing in the present work suggests that substantial modifications are required.

Family **LEPTELLINIDAE** Ulrich & Cooper 1936

As stated above, the Leptellinidae can be divided into three subfamilies, the Leptellininae, the Leptellinae and the Leptestiininae, of which the Leptellinae is confined to the Lower Ordovician. Representatives of both the other subfamilies linger on into the Silurian, but, apart from *Leangella*, they are very rare.

Subfamily **LEPTELLININAE** Ulrich & Cooper 1936

Merciella Lamont and Gilbert 1945

1945 *Leptella* (*Merciella*) Lamont & Gilbert : 655.
1965 *Merciella* Lamont & Gilbert ; Williams : H376.

Lamont and Gilbert originally erected *Merciella* as a subgenus of *Leptella* Hall and Clarke, but Williams elevated it to generic rank, since the two are at least as different as the other genera in the family. The genus contains only the type species.

Merciella vesper Lamont and Gilbert 1945

(Plate 1, figs. 1–5)

1945 *Leptella* (*Merciella*) *vesper* Lamont & Gilbert : 655, pl. 4, figs. 7–12.
1965 *Merciella vesper* Lamont & Gilbert; Williams H376.

Lectotype. (Here selected) BU 369, a brachial internal mould, the original of Lamont & Gilbert 1945, pl. 4, figs. 10, 12, figured here Plate 1, figures 1 and 2.

Discussion. There is a full description of the species by Lamont and Gilbert, and this will not be repeated here. The opportunity has been taken, however, to select a lectotype, and to refigure some of the original specimens for comparison. The species is rare, and, so far as is known, confined to the Wych Beds near the Malvern Hills (Ziegler, Cocks & McKerrow 1968 : 750–7). It occurs there at several localities.

leptellininid gen. et sp. indet

(Plate 1, figs. 6–8)

Discussion. When dissolving shells from strophomenide valves in the Gray Collection, two unique valve interiors appeared, one pedicle and the other brachial, from the Woodland Formation, Lower Llandovery (Rhuddanian) of Woodland Point, south of Girvan, Ayrshire. The two specimens (now registered BB 31831–2) were not in the same box, and may not have come from identical horizons ; however the brachiopod-bearing part of the Woodland Formation is quite thin and was probably deposited quickly, and so the two valves must be of an essentially similar age.

Both specimens probably belong to the same species, as there are unlikely to be two different unknown genera of the same subfamily present at the same locality ; although the possibility must be kept in mind that they might be unrelated. They may be ascribed with some confidence to the subfamily Leptellininae on account of their general interior arrangement, which includes a distinct platform and a dorsal median septum. They are not closely related to *Merciella* (see same plate for comparison), as they differ not only in their general interior proportions, but also in the relative flatness of both valves. In addition the small size of the platform precludes reference to any known genus or species. The specimens look as if they warrant new generic and specific taxa ; however the erection of these on the scanty material available would not be desirable.

Dimensions (in mm)

	l.	w.
BB31831, pedicle internal mould	9·2	13·4
BB31832, brachial internal mould	approx. 9	13·4 (estimated)

Subfamily **LEPTESTIININAE** Havlíček 1961

There are eight nominal genera and subgenera in the subfamily Leptestiinae, *Leptestiina* Havlíček 1952 (M.–U. Ord.), *Bilobia* Cooper 1956 (M. Ord.–U. Ord.), *Diambonia* Cooper & Kindle (M.–U. Ord.), *Leangella* Öpik 1933 (M. Ord.–U. Sil.), *Leangella* (*Opikella*) Amsden 1968 (Wenlock), *Sampo* Öpik 1933 (U. Ord.), *Tufoleptina* Havlíček 1961 (Wenlock), and *Mezounia* Havlíček 1967 (Wenlock). As may be seen, four of these occur in the Silurian, whilst the other four appear to be confined to the Ordovician. In this study *Tufoleptina* is considered a synonym of *Leangella* and *Opikella* retains the subgeneric rank which Amsden proposed for it. The genus *Mezounia* (Havlíček 1967 : 31, pl. 2, figs. 7–10, 13–15) is represented only by its type species, *M. bicuspis* (Barrande 1879), from several localities in the Bohemian Liteň Shales (Wenlock). It is a small form, 6·5–8·5 mm wide, but shows a clearly-developed platform and subperipheral rim. As yet no material attributable to the genus is known, apart from that used in the original description, and its phylogenetic position is enigmatic.

Havlíček (1967 : 29) also places *Tetraodontella* Jaanusson (1962 : 1) within the Leptestiininae, but its brachial valve interior is unlike the rest of the group, and I follow Williams (1965 : H376) in placing it with *Isophragma* Cooper 1956.

Leangella Öpik 1933

1928 *Leptelloidea* Jones *pars* (*non Leptelloidea* s.s.) : 385.
1933 *Leangella* Öpik : 42.
1953 *Leangella* Öpik : 14.
1961 *Tufoleptina* Havlíček : 447.
1965 *Leangella* Öpik ; Williams : H378.
1965 *Tufoleptina* Havlíček ; Willliams : H378
1967 *Tufoleptina* Havlíček : 33.
1968 *Leangella* (*Opikella*) Amsden : 48.

TYPE SPECIES (by original designation) : *Plectambonites scissa* (Salter) var. *triangularis* Holtedahl 1916, the subspecies elevated to species rank as *Leangella triangularis* (Holtedahl) by Öpik (1933 : 42).

DISCUSSION. As well as the type, Öpik put four species into his new genus, *L. scissa* (Salter), *L. segmentum* (Lindström), *L. sholeshookensis* (Jones) and *L. septata* (Cooper). Since that time Cooper & Kindle (1936 : 356) erected the genus *Diambonia* for species similar to *Leangella*, but with a median septum in the pedicle valve, which would include *septata*. The type specimens (GSM 37538, GSM Pg162, GSM Pg225, and GSM Pr107) of *L. sholeshookensis* from the Upper Ordovician Slade Beds of Carmarthenshire have been re-examined ; the species is not a *Leangella* or *Diambonia*, and may even lie outside the subfamily. Another species, *discuneata*, originally described as a *Leangella* (Lamont 1935 : 315), from the Lower Drummuck Group (Ashgill) of Girvan, Ayrshire, possesses a median septum in the pedicle valve, and is here transferred to *Diambonia*. The type specimens are re-illustrated here (Plate 1, figs. 9, 10). True *Leangella* does, however, exist in the Ordovician, for example *Leangella hamari* Spjeldnaes (1957 : 81, pl. 2, figs. 1–3). As far as is known, *Diambonia* became extinct before the close of the Ordovician, as did *Sampo*, which has a denticulate hinge line.

In 1961 Havlíček erected the genus *Tufoleptina*, with type and only species *T. tufogena* Havlíček from the ashy Wenlock Upper Liteň Shales in Bohemia. Havlíček (1967 : 33) states that the genus is extremely close to *Leangella*, but differs " because a conspicuous submarginal ridge is developed in its pedicle valve, which in *Leangella* is absent. " In fact, however, this ridge is variably developed in *Leangella* (e.g. Plate 2, fig. 2), and even occurs in topotype specimens of *Leangella triangularis* itself (Öpik 1933, pl. 8, fig. 6 shows the ridge clearly). Thus the two genera are placed in synonymy. Dr. Havlíček kindly led me to the type locality of *Leangella tufogena*, where a good sample was obtained (Plate 4, figs. 5, 6) which clearly demonstrates its close relationship with the contemporary *Leangella segmentum*, but differences in proportion and shape of the subperipheral rim are enough to keep the two species separate.

Amsden (1968 : 48) has erected a subgenus of *Leangella*, named *Opikella*, with, as type and only species, *L.* (*O.*) *dissiticostella* Amden from the Wenlock St Clair and Clarita Limestones of Arkansas and Oklahoma. It is said to differ from *Leangella* s.s. in having no secondary parvicostellae between the primary costellae. No other species of *Leangella* examined by the present writer lacks these secondary costellae, although in many individuals they cannot be seen owing to indifferent preservation. Thus it seems best to endorse Amsden's choice of subgeneric rank for *L.*(*O.*) *dissiticostella*, illustrating the close relationship between *Opikella* and *Leangella* s.s.

Although Foerste (1903 : 708) did not illustrate his *Plectambonites tennessensis* from the Waldron Shale, near Clifton, Tennessee, Dr. G. A. Cooper has kindly sent over a batch of specimens (BB 31843–54) on exchange labelled *Leangella tennessensis*. They are from a quarry in the Waldron Shale, on Tennessee Route 13, 1·1 miles north of the junction with U.S. highway 64, north of Waynesboro, Tennessee. The species may be definitely attributed to *Leangella* s.s (it certainly has secondary parvicostellae

and seems very close to *Leangella tufogena*, rather than *L. segmentum*, both of which are contemporary.

Species assigned to Leangella

L. triangularis (Holtedahl 1916)
L. (*Opikella*) *dissiticostella* Amsden 1968
L. hamari Spjeldnaes 1957
L. ino Öpik 1953
L. scissa [Salter MS] (Davidson 1871) = *L. woodlandensis* (Reed 1917)
L. segmentum [Angelin MS] (Lindström 1861)
L. tennessensis (Foerste 1903)
L. tufogena (Havlíček 1961)

Leangella triangularis (Holtedahl)

1916 *Plectambonites scissa* (Salter) *triangularis* Holtedahl : 84–5, pl. 15, figs. 5–6.
1933 *Leangella triangularis* (Holtedahl) Öpik : 42–48, pl. 8, figs. 6–8, pl. 9, figs. 1–4.

Discussion. Öpik has already described *Leangella triangularis* so well that a further detailed description will not be given here. There are however one or two small points to make. Öpik describes and illustrates (1933 text-fig. 7 and pl. 9, fig. 2) calcareous outgrowths on the exterior of both valves, which he terms (1933 : 46) comae. I have looked without success in British species for this structure, although admittedly most contemporary material is from clastic rock, rather than the limestones typical of the Baltic region. Öpik describes the comae as having a mass many times larger than the shell which carries it, and as being a rock-forming factor. I have shown Öpik's illustrations to Dr. G. F. Elliott, who considers that these comae may very well be adherent calcareous algae, rather than true outgrowths of the brachiopod exoskeleton. However, true comae are apparently recorded in the Plectambonitacea, and are illustrated schemetically for *Bimuria* by Williams (1965 : H78), but there is no evidence that they ever reached the large proportions suggested by Öpik for *Leangella*.

As already noted in the discussion of the genus, *Leangella triangularis* possesses a subperipheral rim near the pedicle valve margin (Öpik 1933, pl. 8, fig. 6), admittedly variably developed, which was the feature which Havlíček thought it lacked when he erected *Tufoleptina*. It is quite clear from Öpik's section (1933, pl. 9, fig. 2) that the purpose of this subperipheral rim was to fit snugly into the corresponding structure in the brachial valve, forming a tight fit when the two valves were closed.

Leangella scissa [Salter MS] (Davidson)

(Plate 1, figs. 11–14, Plate 2, figs. 1–14, Plate 3, figs. 2–11, Plate 4, figs. 1–4)

1866 *Leptaena scissa* Salter MS *in* Ramsay : 267 (*nomen nudum*).
1867 *Leptaena scissa* Salter MS *in* Murchison : 210, 525 (*nomen nudum*).
1871 *Leptaena scissa* [Salter MS] Davidson : 325, pl. 47, figs. 21–23, *non* figs. 24, 25.
1883 *Leptaena scissa* Salter ; Davidson : 170, pl. 12, fig. 22.
non 1916 *Plectambonites scissa* (Salter) var. *triangularis* Holtedahl. : 84, pl. 15, figs. 5, 6.

1917 *Plectambonites scissa* (Salter) Reed : 880, pl. 14, figs. 34, 35.
1917 *Plectambonites segmentum* (Angelin) var. *woodlandensis* Reed : 881, pl. 14, figs. 36–41.
1928 *Leptelloidea scissa* (Davidson) Jones : 481, pl. 25, figs. 8–12.
1933 *Leangella scissa* (Salter) Öpik : 42.
1965 *Leangella scissa* (Salter) ; Williams : H378, fig. 242, 2a–c.

DIAGNOSIS. *Leangella* with relatively few primary costae, diamond-shaped halves of the brachial valve platform and a pyriform subperipheral rim in the brachial valve, variably developed in the pedicle valve.

DESCRIPTION. *Exterior.* Pedicle valve very convex, almost semicircular in lateral profile ; brachial valve concave, though flatter than the pedicle valve. Umbo inconspicuous but the pedicle valve may be slightly enrolled over the hinge line. Valve outline is semicircular to sub-triangular, maximum width at hinge line or slightly anterior of it. Size of apparent adults varies from population to population, from a maximum of less than 4 mm wide (B_3beds (Idwian) of Llandovery) up to 13 mm wide (Newlands Sandstone (Idwian) of Girvan). Ornament parvicostellate, with between 4 and 14 primary costae, with extremely fine costellae between them, invisible in poor specimens. Spacing between primary costae regular ; near the margin other larger ribs sometimes arise by intercalation. Growth lines not usually seen, except near the margins of large valves. Small rugae sometimes developed near the ears, particularly on pedicle valve, but they do not meet medianly or occur over the whole shell. Interareas relatively large, occasionally with strong growth lines parallel to the hinge line, oriented more or less in the same plane as the valve margins and each other. Central structures are as illustrated by Öpik (1933, text-fig. 7a) for *L. triangularis*, apart from the deltidial plate being laterally thinner, and more triangular at the valve apex, rather than having a pointed arch. Brachial valve structures identical, consisting of a prominent central shaft, with edges of lateral processes showing from the exterior, sometimes bifurcating to accommodate the diductor muscle. There are a pair of small discrete chilidial plates. Apical foramen occasionally seen in very well-preserved small specimens, usually slightly off centre.

Pedicle Valve Interior. Hinge line smooth. Strong teeth are widely divergent. Anteriorly they are part of the same structure as weak dental plates, which continue into muscle bounding ridges, which in turn are elevated medianly to form a positive muscle platform. No median septum. Muscle platform mainly of adventitious shell material, and in gerontic specimens two types of markings occur on platform floor, concentric growth lines (up to 20 sometimes visible) and striae (normally only two or three on each half of the platform) running approximately antero-posteriorly, representing the minor subdivisions of the muscles. Growth lines continuous between two halves of platform, over the small median swell, too slight to be termed a ridge. Although differentiation between adductor and diductor fields is not seen in most specimens, it may be observed in some (Plate 2, figs. 9, 13), in which the diductors are small and narrow, sometimes not even extending to the anterior margin of muscle platform, in contrast with the large bulk of the adductor muscles, which occupy most of the platform area. Vascular markings (e.g. Plate 2, figs. 2, 9, 12 and 14) consist of two large trunks commencing from underneath the anterolateral portions of muscle platform, converging slightly centrally, coming a long way

anteriorly and swinging apart at an acute angle, continuing sub-parallel with anterior valve margin, just posterior of the subperipheral rim (when present). They continue right round until they nearly return to the hinge line, usually fading out just laterally of the muscle platform again. From these main trunks small branches come off at right angles anteriorly. Subperipheral rim variably developed ; it can be seen laterally in most specimens, cutting off the cardinal angles, but only rarely extending anteriorly. Size of papillae small for genus.

Brachial Valve Interior. Hinge line smooth. Cardinal process usually trifid with prominent shaft, but occasionally the lateral processes are themselves split. Socket plates prominent, massive and widely divergent, curving round to become sub-parallel with hinge line (Plate 2, fig. 4), although sometimes the socket plates are shorter and stubbier, but projecting further into the pedicle valve (e.g. Plate 3, fig. 4). Socket plates connected by low lateral ridge to platform, which becomes more elevated anteriorly. Antero-lateral margins of platform are straight, apart from slight frilling ; anteriorly changing direction sharply by a right angle or more, before uniting to form a w shape for the whole field (Plate 2, fig. 4). No median septum, but on the platform floor there is a slight swell dividing the attachment area of the adductors. On most specimens radial striae are present on platform floor (Text-fig. 1). The flaring forward of the platform from the valve floor, together with the anterior fold of the platform in the direction of the pedicle valve, combines to form a conical hole under the antero-median part of the platform (seen as a mould in Plate 2, fig. 7), the " Tubus " of Öpik (1933, pl. 9, fig. 4, text-fig. 17). Vascular markings not so impressed as in the pedicle valve, although faint traces run antero-posteriorly (similar to Öpik 1933, pl. 8, fig. 7). Subperipheral rim well developed in all specimens, more pronounced than in pedicle valve : outline pyriform, with marked anterior constriction and gentle slope on its interior, but on side facing valve margins the angle is more abrupt, with the ridge usually nearly perpendicular, sometimes even overhanging.

Type Specimens. Davidson (1871, pl. 47, figs. 21–25) figured five specimens as *Leptaena scissa* ; fig. 21 from the Upper Llandovery of Norbury, Shropshire, England, figs. 22 and 23 from the Lower Llandovery Gasworks Mudstone, Pembrokeshire, Wales and figs. 24 and 25 from the " Caradoc ; Sholes Hook ", also of Pembrokeshire. Thus the originals of all these figures are available as syntypes. However, Jones (1928 : 48 *et seq.*) discussed the nomenclatorial and identification problems, and removed the Ordovician specimens (Davidson's figs. 24 and 25) to *Sowerbyella quinquecostata*. He also talked of "the type locality at the Gasworks, Haverford-west ", but failed to designate any type specimen. Since that time the Gasworks has been taken as the type locality for *L. scissa*, and so I here formally select the original of Davidson 1871, pl. 47, fig. 23 as lectotype. Davidson's original is also the same pedicle valve internal mould (GSM 11364) which was figured by Jones (1928, pl. 25, fig. 8). The originals of Davidson's figs. 21 and 22 seem to be lost, although the original of Davidson 1883, pl. 12, fig. 22, from Hope Quarry, Shropshire, is in the Davidson Collection (B 13673, Plate 2, fig. 13).

Localities and material. Gasworks Mudstone (Lower Llandovery, Rhuddanian), lane opposite entrance to the Gasworks, Haverfordwest, Pembrokeshire, Wales.

Grid Ref. SM/9588 1533 (GSM 11364 etc., BB 31824–9, BB 32136–67 etc.) Plate 1, figs. 11–14, Plate 2, figs. 1–4).

A_4 beds (lower Llandovery, Rhuddanian), Cwm Rhyddan quarry, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/7623 3250. (BB 32107 etc.)

Woodland Formation (Lower Llandovery, Rhuddanian), Woodland Point, south of Girvan, Ayrshire, Scotland. Grid Ref. NX/168 952 (B 44618–23, BB 31836, BB 31975–80 etc.) (Plate 2, figs. 5–7).

Newlands Sandstone (Middle Llandovery, early Idwian), Newlands Farm, Craighead Inlier, near Girvan, Ayrshire, Scotland. Grid Ref. NS/2777 0432. (B 73641–4 etc.) (Plate 3, figs. 2–4).

Horizon V_2c (Rhuddanian or Idwian), east bank of River Banwy, west of Upper Hall Farm, near Meiford, Montgomeryshire, Wales. Grid Ref. SJ/1326 1058. (BB 31929–48).

B_3 beds (Idwian), old quarry, south side of Cilgwyn-Myddfai road, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/7605 3093 (BB 32085–94).

Venusbank Formation (late Idwian and early Fronian), Hope Quarry, south of Minsterley, Shropshire, England. Grid Ref. SJ/3551 0208. (B 13673 etc. OUM C9121–39) (Plate 2, figs. 8–14).

Temporary exposure in field near Wilmington, Shropshire. Grid Ref. SJ/3061 0246. (GSM 85282–8) (Plate 3, figs. 5–10).

C_1 beds (Fronian), Sefin Shales, near old footbridge, south of Letty'r-hyddod, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/7418 2812. (BB 32095–106) (Plate 4, figs. 1–4).

C_4 beds (Telychian), quarry on Cefn-Cerig road, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/7741 3235. (BB 31675–6 etc.) (Plate 3, fig. 11).

Dimensions (in mm)

	l.	w.
BB 31824 pedicle internal mould, Gasworks (Plate 1, fig. 11)	5·9	8·3
BB 31825 pedicle internal mould, Gasworks (Plate 2, fig. 2)	6·2	8·3
BB 32158 brachial external mould, Gasworks	3·2	6·0
B 73641 brachial internal mould, Newlands (Plate 3, fig. 4)	approx 8	approx. 13
BB 31855 brachial internal mould, Newlands	2·4	4·8
OUM C9136 pedicle internal mould, Hope Quarry (Plate 2, fig. 14)	8·3	8·9

Discussion. *Leangella scissa* probably evolved into *Leangella segmentum* gradually during the upper part of the Llandovery (Telychian). By preceding Fronian times, populations occur such as that at Wilmington, Shropshire (Plate 3, figs. 5–10) which although referable to *L. scissa*, yet contain occasional individuals (Plate 3, figs. 9, 10) which possess circular ω, as opposed to w shaped platforms, although the pyriform shape of the subperipheral rim in the same individual is typical of *L. scissa*. By early Telychian times, however, populations may be found with the characteristic

semi-circular subperipheral rim of *L. segmentum*, although the form of the platform of the figured specimen (Plate 3, fig. 11) is still close to *L. scissa*. How foreign species such as *L. triangularis*, *L. tufogena* and *L. tennessensis* fit into this pattern is not certain ; only one population of each has been available for this study. These three species have not yet been reported from outside their topotypic formations, so that further work could reveal them as varietal populations of the *scissa-segmentum* stock. Fortunately for nomenclature, *scissa* and *segmentum* are the two senior species names in *Leangella*.

The occurrence of *Leangella* is variable, in many apparently favourable localities it is quite absent, at other times it occurs rarely (in many other localities than detailed above), and occasionally in abundance, such as in some horizons of the Hughley Shale of the Church Stretton boreholes (Cocks & Rickards 1969).

Leangella segmentum [Angelin MS] (Lindström)

(Plate 3, fig. 1, Plate 4, figs. 7–12)

1861 *Leptaena segmentum* Angelin Lindström : 374.
1871 *Leptaena segmentum* Angelin ; Davidson : 321, pl. 48, figs. 28–30.
non 1883 *Leptaena segmentum* Angelin var. *cornuta* Davidson : 166, pl. 12, figs. 1–3.
non 1917 *Plectambonites segmentum* (Angelin) var. *woodlandensis* Reed : 881, pl. 14, figs. 36–41.
1928 *Leptelloidea segmentum* (Lindström) Jones : 485, pl. 25, figs. 13–18.
1933 *Leangella segmentum* (Lindström) Öpik : 42, text-fig. 8.
1965 *Leangella segmentum* (Lindström) ; Williams : H378, fig. 242, 2d.

Diagnosis. *Leangella* with as many as 20 primary costae, ω shaped brachial valve platform and approximately semicircular subperipheral rim in the brachial valve, variably developed in the pedicle valve.

Description. *Exterior*. Pedicle valve convex, though normally less than *L. scissa* ; brachial valve concave. Umbo variably developed, often inconspicuous. Enrollment of pedicle valve over hinge line less than *L. scissa*. Valve outline semi-circular, maximum width at hinge line, or just anterior to it. Size range comparable with *L. scissa*, with width only rarely exceeding 10 mm. Ornament parvicostellate, with between 8 and 20 primary ribs with fine costellae between them. Although most of the larger ribs originate at the umbo, some also arise by intercalation anteriorly, more than in *L. scissa*, apparently causing the difference in numbers of larger ribs. Growth lines usually inconspicuous, except near anterior margin, but may rarely be seen over most of valve (Plate 4, fig. 7). Occasionally very prominent growth lines occur, anterior of which costae may be laterally displaced (also seen on Plate 4, fig. 7), presumably as a result of damage or modification of individual setae during mantle regression (perhaps due to adverse conditions or a breeding pause) and different positioning when mantle transgression resumed. Small rugae occasionally developed, confined to lateral extremities. Interareas relatively large, orientation similar to that found in *L. scissa* (Plate 4, fig. 8), apart from the small pair of deltidial plates, which appear to be closer in shape to those in *L. triangularis*. Apical foramen preserved more often than in *L. scissa* ; protegular node often seen in the pedicle valve.

Pedicle Valve Interior. In the type collection from Djupvik there are only three pedicle interiors, of indifferent preservation, but good enough to substantiate the following, chiefly based upon English material from the Wenlock Limestone and Buildwas Beds.

Hinge line smooth. Teeth strong and divergent, continuing weakly anteriorly as dental plates, themselves continuing round as the muscle platform. Outline of platform bilobed. No median septum. Muscle platform floor has same structures, growth lines and radial striae as *L. scissa*. Muscle scars also similar to *scissa*, with most of platform area occupied by adductor scars. Vascular markings occasionally seen as a pair of double mantle canals running anteromedianly from beneath anterior edges of muscle platform lobes rarely seen to swing round parallel to the valve margin. Subperipheral rim parallel with valve margin, often well impressed, particularly in Wenlock Shale material. The taleolae sometimes prominent, particularly in the region just posterior of the subperipheral rim.

Brachial Valve Interior. Hinge line smooth. Cardinal process trifid posteriorly (Plate 4, fig. 8), but anteriorly bifurcating and recombining, to forming slight depression and then central swell in the platform. No median septum. Strong socket plates connected anteriorly with platform. Considerable variation in shape, proportions, relative size and antero-median fold strength of the platform even within a population (Plate 4, figs. 9–12). Strong subradial striae often on the platform. Vascular markings occur parallel ridges running antero-posteriorly from anterior edge of the platform, occasionally to the edge of the subperipheral rim. On the trail there are variable grooves corresponding with the external main costae (Plate 4, figs. 10, 11). Subperipheral rim strong, usually uniformly semi-circular, but rarely with the anterior pyriform stricture so strongly developed in *L. scissa*. Coarse papillae outside platform and inside subperipheral rim, but fine papilla on the trail.

Type specimens. Lectotype (here chosen) Naturhistoriska Riksmuseet, Stockholm, RMS Br 31598, a brachial valve showing the interior (Plate 4, fig. 11) from the Mulde Marl (Upper Wenlock) of Djupvik, Gotland, Sweden. The specimen was collected and labelled by Angelin as "*Leptaena segmentum* Ang." and curated by Lindström (RMS Br 31598–701), thus available to the latter as syntype material in 1861.

Dimensions (in mm.)

	l.	w.	h.
All the specimens are from Djupvik.			
RMS Br 31598 brachial valve, lectotype (Plate 4, fig. 11)	5·3	8·2	—
RMS Br 31602 conjoined valves (Plate 4, figs. 7, 8)	5·2	8·5	1·9
RMS Br 31603 ,, ,,	5·7	10·0	2·3
RMS Br 31604 ,, ,,	5·9	8·7	2·3
RMS Br 31605 ,, ,,	5·6	9·6	2·3
RMS Br 31606 ,, ,,	3·5	6·9	1·1

Discussion. *Leangella segmentum* is a widely quoted species from many stratigraphical levels within the Silurian. The name is really due to Angelin, who gave away and sold many specimens labelled *segmentum* in sets of fossils from Gotland from the 1830's onwards, but it was not until 1861 that the name was properly published (by Lindström), and even then without illustration. The present illustrations (Plate 4, figs. 7–12) are the first of Gotland material, despite the appearance of the name in many faunal lists (e.g. Hede 1960). The opportunity has also been taken to select a lectotype.

The vertical range of the species is not entirely certain. As discussed above, *L. segmentum* probably evolved from *L. scissa* during the late Landovery, and the form occurring in the Telychian Hughley Shales of Shropshire is closer to *segmentum* than to *scissa*. During the Wenlock, *Leangella segmentum* flourished in local swarms, particularly in muddy environments, such as the Lower Wenlock Buildwas Beds of Shropshire and in parts of the Upper Wenlock Mulde Marl of Gotland. The species also occurs rarely in limestones (Plate 3, fig. 1). British Wenlock forms and their distribution will be dealt with by Dr. M. G. Bassett in the course of his forthcoming monograph. He has discovered a population in the Wenlock Shale of the Usk Inlier, Monmouthshire, Wales, with consistently different internal and external proportions, which may merit subspecific status. *Leangella* is rare in the Ludlow, but is known from at least the lower part of the Series in Wales and the Welsh Borderland. There are no British records from higher horizons than the Eltonian (Shergold & Shirley, 1968).

Family **SOWERBYELLIDAE** Öpik 1930

Williams (1965) includes four subfamiles within this family, the Sowerbyellinae Öpik 1930, the Ptychoglyptinae Cooper 1956, the Aegiromeninae Havlíček 1961 and the Xenambonitinae Cooper 1956. All four were flourishing by Middle Ordovician time, but only the Sowerbyellinae and the Aegiromeninae survived to the Lower Silurian. Since these two subfamilies diverged so long before the period of the present study, they will be considered quite separately here.

Subfamily **SOWERBYELLINAE** Öpik 1930

There are at the moment twelve nominal genera or subgenera within this subfamily, as follows:—

Sowerbyella Jones 1928, type species *S. sericea* (J. de C. Sowerby)
Viruella Rõõmusoks 1959, type species *V. liliifera* (Öpik)
Anisopleurella Cooper 1956, type species *A. tricostellata* Cooper
Eochonetes Reed 1917, type species *E. advena* Reed
Eoplectodonta Kozlowski 1929, type species *E. precursor* (Jones)
Thaerodonta Wang 1949, type species *T. aspera* Wang
Ygera Havlíček 1961, type species *Y. ygerens* Havlíček, a junior synonym of *Y. sowerbyana* (Barrande)

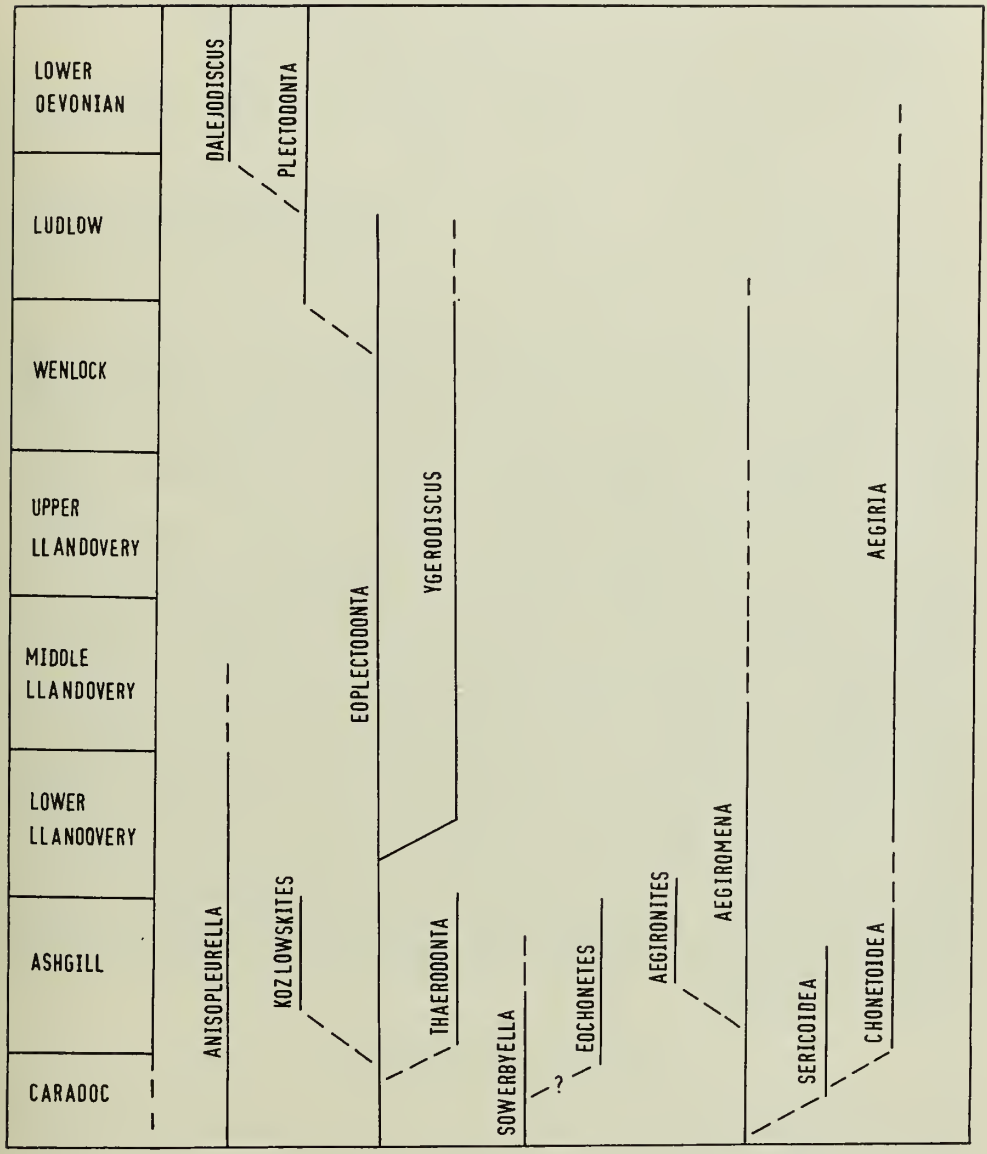

FIG. 6. Possible phylogeny of the Sowerbyellidae from the Upper Ordovician to the Lower Devonian.

Ygerodiscus Havlíček 1967, type species *Y. undulatus* (Salter)
Plectodonta Kozlowski 1929, type species *P. mariae* Kozlowski
Dalejodiscus Havlíček 1961, type species *D. comitans* (Barrande)
Plectodontella Havlíček 1953, type species *P. redunca* Havlíček
Kozlowskites Havlíček 1952, type species *K. nuntius* (Barrande)

Of these genera, only three, *Sowerbyella*, *Viruella* and *Anisopleurella*, do not bear denticles on the hinge line, and all these have their type species from near the base of the Caradoc. A fourth genus *Eochonetes*, whilst not denticulate, has a most distinctive perforated hinge line. In the examination of a large number of populations of Sowerbyellinae, no population has been seen from the Silurian which does not possess a denticulate hinge line. Thus, contrary to previous records, it seems likely that *Sowerbyella* became extinct before the close of the Ordovician and that all Llandovery and later Sowerbyellinae may be referred to *Eoplectodonta* and its later derivatives, namely *Ygerodiscus*, *Plectodonta*, *Plectodontella* and *Dalejodiscus*. The last two genera have only been recorded from the post-Ludlovian of Europe, and it is also possible that *Plectodonta* may be post-Ludlovian, although the Upper Silurian faunas have not yet been closely studied, apart from in Bohemia. The only exception is *Anisopleurella*, a chiefly Ordovician genus with a smooth hinge line, which lingered on to occur rarely in the Silurian.

There can be no doubt that some sowerbyellids have highly developed plicae, whilst others do not. This was recognized in Jones's division (1928 : 397) of *Sowerbyella* into various groups, chiefly based on the external form of the shell. The plicate group Jones termed the '*undulata*-group' and this seems essentially the basis upon which Havlíček (1967) erected his new genus *Ygerodiscus*, with *undulata* as type species. This genus is accepted as valid in the present paper. However, there is always some variability in shell undulation, as there is also in rugation. In every population examined there are some individuals showing rugae in the posterior region, sometimes confined to the ears, sometimes spread some way along the hinge line, and in occasional individuals an odd ruga may go right across the whole shell. This rugation cuts across the radial ornament, in contrast with one of Jones's other groups, the ' subcorrugatella group ' in which the small rugae are interrupted by the costellae, a form of ornament seen elsewhere in the Plectambonitacea, for example in *Pytchoglyptus*, and which homoeomorphically arises in other groups of the Strophomenida, for example in the strophomenaceans *Pentlandina* and *Cyphomena* (*Cyphomenoidea*) (Cocks 1968).

Eoplectodonta Kozlowski 1929

1929 *Plectodonta* (*Eoplectodonta*) Kozlowski : 112.
1956 *Eoplectodonta* Cooper : 807.
1961 *Ygera* Havlíček : 449.
1965 *Eoplectodonta* (*Eoplectodonta*) Williams : H381.
1967 *Ygera* Havlíček : 58.

Type species (by original designation) ; *Sowerbyella precursor* Jones 1928, from the Lower Llandovery of Pembrokeshire, Wales. As outlined below, this species is

considered here as a junior subjective synonym of *Leptaena duplicata* J. de C. Sowerby (*in* Murchison 1839).

Discussion. *Eoplectodonta* is treated here as a genus separate from *Plectodonta*, rather than as the subgenus originally created by Kozlowski. The differences between the two genera are as follows (the observations on *Plectodonta* are based on topotype material of *P. mariae*, B. 81370–8 (figured here Plate 16, figs. 10–12), sent to the British Museum in an exchange with the University of Warsaw in 1932).

Plectodonta	*Eoplectodonta*
Non-alate, with rounded hinge margins	Alate
Umbo not incurved, open cardinal area	Enrolled hinge line in adults
Deltidium present, with reduced chilidium	Open delthyrium, with conspicuous chilidial plates

That *Plectodonta mariae* is only developed to half the usual size of *Eoplectodonta*, and also possesses more than double the number of primary costellae, are regarded as specific, rather than generic, features. In addition *P. mariae* is much more strongly papillose in the interior than *Eoplectodonta*, more approaching the condition seen in *Aegiria*, but this too may be merely a specific character. The general arrangement of the brachial valve interiors, although differing in the relative emphasis of some structures, is, however, essentially similar in both genera, and the descent of one from the other at some time in the late Silurian seems highly probable.

In the Treatise on Invertebrate Paleontology, Williams (1965) put *Thaerodonta* Wang into synonomy with *Eoplectodonta*, and *Kozlowskites* Havlíček as a subgenus of the latter. Both these other genera are known only from the Upper Ordovician. *Kozlowskites*, known only from the Ashgill of Bohemia, differs from *Eoplectodonta* in some relatively minor details of the pedicle valve, as discussed by Havlíček (1967 :56), and Williams' subgeneric arrangement seems correct. However in the present paper *Thaerodonta* is retained as generically distinct from *Eoplectodonta* as it differs fundamentally in having denticles in the brachial valve and fossettes in the pedicle valve as opposed to the other way round in *Eoplectodonta* (Wang 1949 : 19, pl. 11).

Apart from *Ygerodiscus*, discussed below, the only other Silurian genus closely related to *Eoplectodonta*, is *Ygera* Havlíček (1961, 1967). To this genus Havlíček (1967 : 58) refers four species, *Y. sowerbyana* (Barrande), *Y. bidecorata* (Barrande), both from the Bohemian Wenlock, and *Y. lata* (Jones) and *Y. transversalis* (Wahlenberg), from the Wenlock of England and Gotland respectively. In addition Havlíček attributes " *Y.* cf *lata* (Jones 1928) ; Llandovery, U.S.S.R. (Podolia) " (Nikiforova 1954 : 76, pl. 7, figs. 1, 2). He states that " *Eoplectodonta* differs from the related genus *Ygera* in the presence of a well-developed median septum in the brachial valve and ill-defined lobes of visceral field. . . . *Thaerodonta* fairly resembles *Ygera* ; it is mainly distinguished in having small teeth on the cardinal margin of brachial valve, while in *Ygera* the case is opposite, as the denticulate cardinal margin occurs in the pedicle valve " (Havlíček 1967 : 58).

Dr. Havlíček was kind enough to lead me to the locality Hliník in Bohemia (the type locality of his earlier *Ygera ygerens*, which he subsequently put into the synonomy of *sowerybana*) where a large sample of *Ygera* was obtained (Plate 13, figs. 2,

4–6, 8, 9). Contrary to his report, denticles do occur in the pedicle as well as the brachial valve. The septal structures are variable, but within the range of variability of *Eoplectodonta*. Thus, although *sowerbyana* may be recognized as a distinct species, *Ygera* is regarded in this paper as a junior synonym of *Eoplectodonta*.

The following Silurian species are assigned to *Eoplectodonta* :—

Leptaena duplicata J. de C. Sowerby 1839 (synonyms *Plectambonites mullochensis* Reed 1917, *Plectambonites tricostata* Reed 1917, *Sowerbyella precursor* Jones 1928, *Sowerbyella superstes* Jones 1928).

Anomites transversalis Wahlenberg 1819.

Plectambonites penkillensis Reed 1917 (synonyms *Sowerbyella millinensis* Jones 1928, *Sowerbyella canastonensis* Jones 1928, *Sowerbyella parabola* Jones 1928).

Leptaena duvalii Davidson 1847 (the Wenlock " *transversalis* " of many authors ; synonym *Sowerbyella lata* Jones 1928).

Leptaena sowerbyana Barrande 1848 (synonym *Ygera ygerens* Havlíček 1061).

Strophomena bidecorata Barrande 1879.

The following species may be referable to *Eoplectodonta*, but have not yet been re-investigated :—

Sowerbyella elegans Poulsen 1943 : 16, pl. 2, fig. 4. Upper Llandovery (*sedgwickii* Zone), Offley Island, Greenland.

Plectambonites tenera Shaler 1865 : 64, no illustration (put in synonomy of *transversalis* by Twenhofel 1928 : 192). Gun River and Jupiter Formations (Middle and Upper Llandovery), Anticosti Island, Canada.

Sowerbyella minuta Kul'kov 1967 : 67, pl. 1, figs 7–9. Upper Wenlock of the Altai Highlands, U.S.S.R.

Plectodonta exceptionis Rybnikova 1967 : 189, pl. 19, figs. 8–12. Lower to Middle Landovery from boreholes in Latvia, U.S.S.R.

Of these last four species, *elegans* appears from Poulsen's illustrations to be small *Eoplectodonta*—the form of the adults remains unknown, and *tenera* requires proper definition and illustration. *P. exceptionis* is adequately illustrated, and may be a distinct species, probably related to *E. penkillensis*. *S. minuta* is poorly described and illustrated, and although it appears to be a sowerbyellid, the figures are too poor and description too general to say more.

There is also a small group of species which have been described from the Upper Silurian or Lower Devonian of central Europe :—

Leptaena minor Roemer 1854 : 12, pl. 3, fig. 1.

? *Plectambonites minor* var. *digitata* Wolburg 1933 : 53, pl. 2, fig. 6.

Plectodonta minor var. *alatiformis* Schmidt 1939 : 83, text-fig. 6.

Plectodonta thuringica Schmidt 1939 : 80, pl. 3, figs. 1–2.

It is quite possible that some of these names are synonyms of each other, but the genus to which they belong is uncertain, and the whole of this small group is in need of revision, together with the distribution of *Plectodonta* itself.

Eoplectodonta duplicata (J. de C. Sowerby)

(Plate 5, figs. 1–12, Plate 6, figs. 1–13, Plate 7, figs. 1–11, Plate 8, figs. 1–11)

1839 *Leptaena sericea* var. J. de C. Sowerby *in* Murchison : 636, pl. 19, fig. 2.
1839 *Leptaena duplicata* J. de C. Sowerby *in* Murchison : 636, pl. 22, fig. 2.
1871 *Leptaena transversalis* (Wahlenberg); Davidson *pars* : 318, *non* pl. 48, figs 1–9.
1917 *Plectambonites transversalis* (Dalman) ; Reed : 886, pl. 15, figs. 35, 36.
1917 *Plectambonites transversalis* var. *duvali* (Davidson) ; Reed : 887, pl. 15, figs. 37–40.
1917 *Plectambonites transversalis* (Dalman) var. *mullochensis* Reed : 887, pl. 15, figs. 41, 42, pl. 16, figs. 1, 2.
1917 *Plectambonites transversalis* (Dalman) var. *tricostata* Reed : 889, pl. 16, fig. 8–13.
1928 *Sowerbyella duplicata* (J. de C. Sowerby) Jones : 432, pl. 22, figs. 6–13, pl. 23, figs. 1, 2.
1928 *Sowerbyella precursor* Jones : 437, pl. 23, figs. 3–5.
1928 *Sowerbyella mullochensis* (Reed) Jones : 439, pl. 23, figs. 6–9.
1928 *Sowerbyella superstes* Jones : 441, pl. 23, figs. 10–12.
1928 *Sowerbyella undulata* (Salter) Jones : *pars* : 452, pl. 24, figs. 4–6, *non* fig. 3.
1928 *Sowerbyella undulata* (Salter) var. *tricostata* (Reed) Jones : 458, pl. 24, figs. 8, 9.
1929 *Plectodonta duplicata* (J. de C. Sowerby) Kozlowski. : 113
1929 *Plectodonta mullochensis* (Reed) Kozlowski : 113.
1929 *Plectodonta superstes* (Jones) Kozlowski : 113.
1929 *Plectodonta* (*Eoplectodonta*) *praecursor* [*sic*] (Jones) Kozlowski : 113.
1965 *Eoplectodonta* (*Eoplectodonta*) *praecursor* [*sic*] (Jones) Williams : H380, fig. 243, 5a–c.

Diagnosis. Often large *Eoplectodonta* which are usually relatively wide, with a short median septum in the pedicle valve. Despite considerable variation within populations, most individuals have a fairly well developed median septum in the brachial valve. Many individuals possess slight *Ygerodiscus*-like undulations, and on the pedicle valve exterior there is usually a prominent central costa with two small undulations on each side of it which die away quickly anteriorly.

Description. *Exterior.* Pedicle valve very convex, semicircular in lateral profile, with a very concave brachial valve. Pedicle valve enrolled over hinge line, pedicle valve umbo incurved ; there is a concave hollow at the brachial valve umbo apart from the tiny protegular node. Outline alate to semicircular (compare Plate 5, fig. 10 with Plate 6, fig. 7 from the same population), but length seldom exceeds valve width. Maximum width hinge line, or slightly anterior in a few specimens ; very variable, even within a population, but often exceeding 20 mm. Ornament variable, normally unequally parvicostellate with about 200 costae in adult specimens and up to 15 small costellae between each costa (Plate 5, fig. 1), however in some specimens (e.g. Plate 6, figs. 10, 11) the distinction between the two types of rib breaks down, and the whole valve appears to be covered with costellae of a more or less uniform size. On pedicle valve exterior there is a stronger median costa, with two small undulations on each side which die out quickly anteriorly, usually within 2 mm of the umbo. This feature is particularly noticeable on young individuals (Plate 8, figs. 1, 2), which is why Reed was misled into giving the separate trivial name *tricostata* to such young forms. Sometimes undulate (e.g. Plate 7, figs. 1, 2), but within a population there is complete gradation between unulate and smooth specimens. Growth lines sometimes visible. Small rugae often developed in the region close to the ears. The interareas are set at an obtuse angle under the incurved pedicle valve. Oblique traces of the denticle growth tracks can be seen from the

outside of the interareas as well as the normal growth lines parallel to the hinge line. Margins of delthyrium diverge at an angle of between 90 and 110 degrees (Text-fig. 3a). No deltidial plates. Pair of small discrete chilidial plates set at a slight angle to the interarea, between which may be seen the posterior face of the cardinal process. Central shaft completely visible, also two lateral processes, the bases of which are partly hidden behind chilidial plates. Very small apical foramen sometimes visible, mostly, however, it appears to have been plugged by calcite.

Pedicle Valve Interior. Hinge line denticulate for approximately half its length, although sometimes as much as three-quarters. No real teeth, although in some specimens the central part of the hinge line projects slightly anteriorly on each side of the delthyrium, forming a very slight swell, analagous to the composite plates of some stropheodontids. Flaring away at the same angle as the sides of the open delthyrium are a pair of small dental plates fused to the valve floor acting as posterior muscle bounding ridges. Small median septum confined to the very posterior end of the valve bifurcating and then dying out posteriorly of the anterior of the muscle bounding ridges. Muscle scars strongly impressed, divergent from each other at 50 to 80 degrees. No striae on muscle field.

Vascular system often well impressed consisting of pair of main trunks running from anterior part of muscle field, which subdivide many times, but with a high degree of variability (see Text-fig. 5, also Plate 6, figs. 1, 3, 7, 8 and Plate 8 figs. 3, 4). Valve interior often highly papillate, except postero-medianly.

Brachial Valve Interior. Fossettes on the hinge line corresponding to denticles on pedicle valve. Cardinal process prominent, trifid when viewed from the posterior, with central shaft and two lateral processes, separated by grooves. Viewed from above, cardinal process bifurcates anteriorly and merges with flaring clavicular plates, not so large as *Eoplectodonta* aff. *duvalii* (Plate 12, figs. 14, 15). Median septum usually present, of variable strength, sometimes strong and running a long way anteriorly (Plate 5, fig. 4), at other times no more than the residual ridge between two callouses (Plate 5, fig. 6). Inner side septa usually strong and well-developed, growing initially perpendicular to the valve floor, then curving over laterally in larger specimens. Outer side septa variably developed, sometimes almost absent in smaller specimens (Plate 6, fig. 9), at other times massive (Plate 5, figs. 5, 11) and occasionally grotesque, with spreading tops (Plate 6, fig. 5) which are club-shaped in section. Bema also variable, invisible in young specimens except as an area without large papillae, and poorly developed in many full grown individuals (Plate 5, figs. 9, 10), but usually entire, apart from anterior interruption by the vascular system (seen well in Plate 5, figs 3, 6) ; its antero-median edge runs from anterior edges of outer side septa posteriorly to fuse with anterior edges of inner side septa to give an overall bilobed and petoloid shape to the central field. Vascular system is variable in detail, one set is seen well in the individual of Plate 5, figs. 3 and 6. Valve interior highly papillose outside the smoother central field.

Type specimens. The holotype is GSM Geol. Soc. Coll. 6874 (Plate 5, fig. 2), the original of J. de C. Sowerby (in Murchison 1839) plate 22, fig. 2. The locality label glued to the specimen reads " cefn rhyddan, Llandovery ", in Murchison's hand-

writing, although the localities given in the text (1839 : 636) are " Cefn, near Welshpool ; Robeston Wathen, Pembrokeshire ". The specimen may be definitely recognized as the original of the figure, since it is distinctively broken, and also possesses well-preserved vascular markings, both features reproduced on the plate. The grey siltstone matrix excludes Robeston Wathen, and is closer to other material from Cefn Rhyddan than from Cefn, near Welshpool, and the text locality is probably an error for Cefn Rhyddan, a small quarry in the A_4 beds of Llandovery.

Localities and material. A_4 beds (Lower Llandovery, Rhuddanian), Cefn Rhyddan quarry, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/7622 3248. (GSM Geol. Soc. Coll. 6874, 6877, BB 31668) (Plate 5, figs. 1, 2).

Gasworks Mudstone (Lower Llandovery, Rhuddanian) Pembrokeshire, Wales.

(i) opposite entrance to the Gasworks, Haverfordwest, Grid Ref. SM/9588 1533. (GSM 37568, 37571–3 etc., BB 31684–31759, BB 31670–4 etc.) (Plate 5, figs. 3–12, Plate 6, figs. 1–8).

(ii) north end of railway cutting, 150 yards SW of Haverfordwest Station. Grid Ref. SM/9588 1563. (GSM 37567, GSM TCC 1191–1209, BB 32055–78) (Plate 6, figs. 9–14).

(iii) other localities listed by Jones (1928) : Frolic path, 620–625 yards from gate at Higgon's Well, Haverfordwest ; 350 yards WSW of Merlin's Bridge, Haverfordwest ; riverside 99 yards and 218 yards SE of gate at Higgon's Well, Haverfordwest ; old quarry on east side of Black Backs Bridge, 3 miles from Haverfordwest on road to Rhos, and many other localities mentioned in Strahan *et al.* 1914 : 236–7 and Cantrill *et al.* 1916 : 57.

Gasworks Sandstone (Lower Llandovery, Rhuddanian) 20 yards S of wall bounding the old work house grounds, Union Hill, Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/956 152. (GSM 37575–79, GSM Pg2722–37) (Plate 8, figs. 5–8).

Woodland Formation (Lower Llandovery, Rhuddanian), Woodland Point, south of Girvan, Ayrshire, Scotland. Grid Ref. NX/168 952 (B 73537–40, B 73749–50, BB 31830–5, BB 31949–74, BB 31984–91 etc.) (Plate 7, figs. 1–11, Plate 8, figs. 1–4).

Mulloch Hill Formation (Lower Llandovery, Rhuddanian), Mulloch Hill quarry, near Girvan, Ayrshire, Scotland. Grid Ref. NS/2703 0399. (B 44648–9, B 44718–9 etc.) (Plate 8, figs. 9–11).

Dimensions (in mm.)

	l.	w.
GSM Geol. Soc. Coll. 6874, pedicle valve internal (Plate 5, fig. 2), Cefn Rhyddan, holotype	11·6	—
GSM Geol. Soc. Coll. 6877, brachial valve external (Plate 5, fig. 1), Cefn Rhyddan	11·1	19·8
BB 31668 pedicle valve internal, Cefn Rhyddan	7·3	15·5
B 73537 pedicle valve external (plate 8, fig. 1), Woodland Point	3·2	8·5
BB 31958 pedicle valve external, Woodland Point	13·8	20·1
BB 31957 brachial valve external, Woodland Point	8·5	20·8
BB 31960 brachial valve external, Woodland Point	8·4	17·3
BB 31955 brachial valve external, Woodland Point	6·0	15·8

Discussion. Only a small population of *Eoplectodonta duplicata* is known from the type locality near Llandovery, they fall within the variation shown by the large population of approximately the same age from the Gasworks Mudstone, opposite the entrance to Haverfordwest Gasworks, Pembrokeshire, about 50 miles away. Jones (1928) named two species, *precursor*, from the Gasworks Mudstone at another locality (Plate 6, figs. 9–14), and *superstes* from the overlying Gasworks Sandstone of the same area (Plate 8, figs. 5–8). After consideration of both the type specimens and also topotypic collections of these species, they are here placed within the synonomy of *duplicata*. Kozlowski (1929) designated *precursor* (which he mis-spelt *praecursor*) as the type species of *Eoplectodonta*, and so *duplicata* now assumes this role.

In his monograph of the Girvan brachiopods, Reed (1917) erected what he described as new varieties of *Plectambonites transversalis* ; *mullochensis* from the Mulloch Hill Formation (Plate 8, figs. 9–11), which he termed Lower Llandovery, and *tricostata* from Woodland Point (Plate 7, figs. 1–11, Plate 8, figs. 1–4) which he termed Middle Llandovery. From recent collecting and field work by the present writer and Dr. P. Toghill, to be published separately, these two localities are now known to be of virtually identical age, i.e. older than at least part of the *cyphus* Zone of the Lower Llandovery (Rhuddanian). This is similar to the age of the *duplicata* type locality, and the Scottish forms fall within the range of variability of the Welsh species, thus Reed's two names are placed into the synonomy of *duplicata*.

The species, as with many other plectambonitaceans, is extremely variable. For example, the median septum is sometimes barely visible (Plate 5, figs. 3, 6) and at other times most marked (Plate 5, figs. 4, 7).

Eoplectodonta penkillensis (Reed)

(Plate 9, figs. 1–15, Plate 10, figs. 1–12, Plate 11, figs. 1–16)

1868 *Leptaena transversalis* Dalman ; Davidson : 19, pl. 3, figs. 8–13.
1871 *Leptaena transversalis* Dalman ; Davidson : 318 *pars*, pl. 48 figs. 3, 9, *non* figs. 1, 2, 4–8.
1917 *Plectambonites transversalis* (Dalman) var. *penkillensis* Reed : 888, pl. 16, figs. 3–7.
1928 *Sowerbyella penkillensis* (Reed) Jones : 443.
1928 *Sowerbyella millinensis* Jones : 444, pl. 23, figs. 13–16.
1928 *Sowerbyella millinensis* var. *parabola* Jones : 446, pl. 23, figs. 18–20.
1928 *Sowerbyella millinensis* var. *canastonensis* Jones : 447, pl. 23, figs. 17, 21–2.
1929 *Plectodonta millinensis* (Jones) Kozlowski : 113.
1945 *Plectodonta millinensis* cf. var. *canastonensis* (Jones) Lamont & Gilbert : 659, pl. 4, figs. 13–14.

Diagnosis. Smaller *Eoplectodonta* which are relatively wide, and often possess an incurved umbo with a smaller interarea than *E. transversalis*. The brachial valve median septum is usually clearly seen. Very small thin deltidal plates are present on either side of the open delthyrium.

Description. *Exterior.* Pedicle valve convex, brachial valve concave, though often less so than in other species of *Eoplectodonta*. Pedicle umbo moderately prominent and pedicle valve enrolled over hinge line. Outline alate to semicircular.

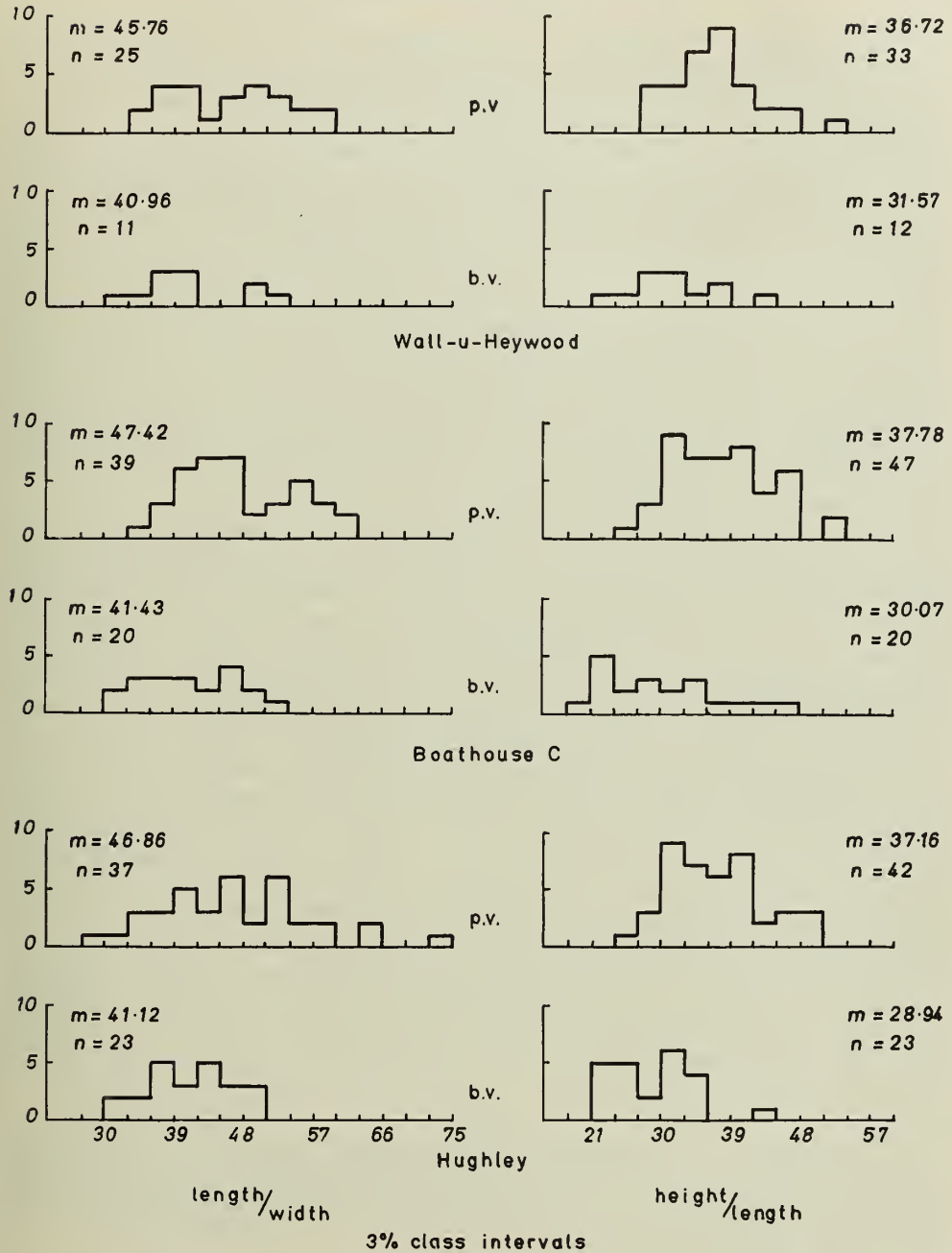

FIG. 7. Variation of *Eoplectodonta penkillensis* in three populations from the Hughley Shale (Telychian) of Shropshire, England. n = number of specimens, m = mean, p.v. and b.v. = pedicle and brachial valves. For detailed localities see text.

Maximum width at hinge line, but alae are often rounded off. Maximum width 16 mm. in over 400 specimens. Ornament unequally parvicostellate with from 8 to 22 larger costae, in between each of which are from 4 to 15 small costellae. Often a slightly stronger central median costa (Plate 11, fig. 15). In some specimens the distinction between the relative strengths of the two ribbing types tends to break down (Plate 10, fig. 7) ; there is also a large amount of variation within one population. Some individuals slightly undulate (Plate 11, figs. 4, 7) but most smooth, the undulation is not as extreme as in *Ygerodiscus* (compare with Plate 15). Small rugae often seen, confined near the hinge line (Plate 10, fig. 7, Plate 11, fig. 15). Growth lines occasionally seen, but not so prominent as on *E. transversalis*. Delthyrium open, but, unlike other species of *Eoplectodonta*, there are a pair of thin bladelike deltidial plates which protrude slightly out from the interarea (Text-fig. 3b). Chilidial plates larger than other species, although still discrete from each other ; their junction with the interarea a smooth curve rather than an angular break. Central shaft of cardinal process is visible from exterior, but bases of two lateral processes are hidden by chilidial plates. Small apical foramen sometimes visible, usually, however, it appears to have been plugged by calcite.

Pedicle Valve Interior. Hinge line denticulate for at least half its length, sometimes nearly all. No teeth but the " composite plate " swelling is again found (Plate 11, fig. 8). Small dental plates flare out anterolaterally, dying away at the side of the muscle field. Small medium septum, confined to the umbonal area, bifurcating anteriorly before merging with the valve floor. Muscle field rhomboidal in shape, with vascular system anterior to it as two long antero-laterally directed mantle canals which split up into many secondary canals more than half-way down the length of the valve. Valve interior often very papillate, except on muscle field.

Brachial Valve Interior. Fossettes along the hinge line, corresponding with pedicle valve denticles. Cardinal process less massive than in *E. duplicata*, and forming posterior wall of a deep pit which extends almost to the valve exterior. Clavicular plates diverge between 85 and 110 degrees. Median septum of variable length (on Plate 10 compare fig. 10 with fig. 12). Inner side septa usually the longest structures inside brachial valve, even in larger specimens (Plate 11, figs. 9, 13), outer side septa are not so large. There are no specimens of *E. penkillensis* on which the outer side septa reach the grotesque proportions seen in *E. duplicata*, *E. transversalis* and *E. duvalii*. Bema variably developed, not usually continuous anteriorly, it often merges with the shell floor lateral to the anterior edge of the side septa, with characteristic curved sides. Vascular system not well known. Valve interior often highly papillose (Plate 10, figs. 4, 12) outside the muscle field.

Type specimens. Lectotype (here chosen) B 44710, a partly exfoliated pedicle valve, the original of Reed 1917 plate 16, fig. 3, collected by Mrs. Gray from "Bargany Pond Burn", Girvan, Ayrshire. This locality is now known to be of Upper Llandovery (Fronian) age and is at a very small stream 200 yards SE of its junction with Lauchlan Burn. Grid Ref NX/2500 9858.

Localities and material. " Camregan Group" (formation name needs revision) (Fronian). The locality called by the Gray family "Bargany Pond Burn ",

actually a small stream which is a tributary of Lauchlan Burn, near Girvan, Ayrshire, Scotland. Grid Ref. NX/2500 9858. (Plate 11, figs 14–16) (B 44710–7 etc).

" Penkill Group " (formation name needs revision, the horizon is very similar to Bargany Pond Burn) (Fronian). The locality called by the Gray family " Penkill ", in a very small brook 550 yards SE of Penkill Castle, near Girvan, Ayrshire, Scotland. Grid. Ref. NX/2360 9832. (B 44599, B 44601, B 44632–44 etc.).

Uzmaston Beds (Telychian), 100 yards NW of Haroldston St. Issells Church, near Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/9636 1409. (Plate 9, figs. 1, 2, 4, 5) (GSM 37556–9, GSM TJ929–78).

Uzmaston Beds (Telychian), near ruins of mill, 200 yards W by N of Millin Farm, 3 miles ESE of Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/9943 1418. (Plate 9, figs. 8, 9, 11, 12) (GSM 37530, GSM 37540–1, BB 32419 etc.).

Canaston Beds (Telychian) road cutting opposite Canaston Farm, near Narberth, Pembrokeshire, Wales (Plate 9, figs. 3, 6, 7, 10) (GSM 37531, BB 32418 etc.).

Canaston Beds (Telychian) south bank of the eastern arm of the Cleddau, east of Haverfordwest, Pembrokeshire, Wales. Grid. Ref. SN/0485 1385. (Plate 9, figs. 13–15, Plate 10, figs. 1–3) (BB 31839, BB 32219–21, BB 32223–8 etc.)

C_5 Beds (Telychian), road cutting opposite Cefn Cerig Farm, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/7746 3229. (BB 31761–31823).

Hughley Shale (late Fronian and Telychian) at the following main localities:—

(i) bank of River Onny, near Wistanstow, Shropshire, England. Grid. Ref. SO/4260 8532. (Plate 10, figs. 7–9, 11, 12) (OUM C11943–77).

(ii) south-west bank of Heath Brook, 500 yards ENE of the Plough Inn, Wall-under-Heywood, Shropshire, England. Grid Ref. SO/5120 9276. (OUM C13003–55).

(iii) stream exposure near Hughley, Shropshire, England. Grid Ref. SO/5605 9747. (Plate 11, figs. 3, 4, 7) (BB 31838, 31840, OUM C13655–735).

(iv) stream exposure 270 yards SW of the house called Domas, near Harley, Shropshire, England. Grid Ref. SJ/5936 0062. (Plate 11, figs. 1, 2) (BB 32222 etc., OUM C13541–654).

(v) stream exposure in Boathouse Coppice, east of Sheinton, Shropshire, England. Grid Ref. SJ/6205 0398. (OUM C12572–657).

Wych Beds (Telychian) bank on south side of football pitch at Cowleigh Park, Malvern Hills, Herefordshire, England. Grid Ref. SO/7616 4723. (A.M. Ziegler Collection OUM C4845–96) (Plate 11, figs. 5, 6, 8–13).

The species occurs in many other localities in the Welsh Borderland, particularly in Shropshire and Montgomeryshire.

Dimensions (in mm.)

	l.	w.
B 44710 pedicle valve, lectotype (Plate 11, fig. 14) Bargany Pond Burn.	7·4	approx. 14
B 44712 pedicle valve internal (Plate 11, fig. 16) Bargany Pond Burn.	8·2	approx. 14
B 44713 pedicle valve internal, Bargany Pond Burn	8·2	11·6
GSM 37531 (first specimen) brachial external mould (Plate 9, fig. 3) Canaston Farm.	6·5	12·1

	l.	w.
GSM 37531 (second specimen) pedicle internal mould (Plate 9, fig. 6) Canaston Farm.	7·1	approx. 12
GSM 37531 (third specimen, on other side of slab from first two) pedicle internal mould, Canaston Farm.	6·9	13·0

Discussion. In the Upper Llandovery of Britain, plectambonitaceans are abundant at many localities. They were usually referred to *Leptaena transversalis*, Reed (1917) erected *penkillensis* as a variety of that species. In 1928 Jones erected a new species, *millinensis*, with two varieties, *parabola* and *canastonensis* from Pembrokeshire, and most subsequent writers have used one or more of these last names.

Apart from the type locality of *millinensis*, an old pit now obscured, collections have been gathered from the type localities of these nominal species and subspecies, and have been considered together with other large collections, mainly from Shropshire and the Welsh Borderland. Text-fig. 7 shows the measurements of the populations at three localities in the Hughley Shale, Wall-under-Heywood, Boathouse Coppice, and near Hughley itself, and show the very large variation in the relative width, length and height. The histograms appear in some cases to have some bimodal arrangement. That this is not taxonomically significant, however, is shown by the fact that individuals from, say, the left of a trough in a height/length ratio histogram, fall quite at random into the corresponding length/width ratio histogram, and vice versa. Despite the very wide range observed, the means of the figures are very similar between the three collections, leaving no room to doubt that only one species is represented in all three cases. The relative strength, and even presence and absence, of some internal structures in the valves was also seen to possess a remarkable range of variation.

Jones originally defined his two " varieties " *parabola* and *canastonensis* (1928: 446–7) on the length/width-proportions, *parabola* being longer and less wide than *canastonensis*. Collections from the two type localities gave the following measurements :

S. millinensis parabola (near old mill, 200 yds W by N of Millin Farm 3 miles ESE of Haverfordwest, Pembrokeshire).

$\bar{l}/\bar{w}$ for 20 pedicle valves 44·9% (OR 33·7–63·4%), $s^2 = 84·6$

$\bar{l}/\bar{w}$ for 27 brachial valves 44·3% (OR 35·7–57·9%), $s^2 = 39·1$

S. millinensis canastonensis (road opposite Canaston Farm, 2½ miles W. of Narberth, Pembrokeshire).

$\bar{l}/\bar{w}$ for 5 pedicle valves 49·0 (OR 38·3–62·7), $s^2 = 85·5$

$\bar{l}/\bar{w}$ for 12 brachial valves 46·8 (OR 35·8–59·8), $s^2 = 46·1$

When significance tests, (in this case ' t ' tests) are applied, the differences between the two collections are insignificant, and on the basis of length/width ratios the two " varieties " cannot be considered separable, even as subspecies. It is unfortunate that *penkillensis* was not well known (the brachial interior was not figured by Reed) at the time of Jones' work as he (1928 : 443) noted that " it bears a considerable resemblance to certain forms which occur abundantly in the Millin Stage of Haverfordwest and Narberth, it is probable that the internal features are also of the same type ".

However, despite the exceptionally wide variability shown by the various species of *Eoplectodonta*, the length/width and height/length ratios of *E. penkillensis* are significantly lower than those of *E. transversalis* (Text-fig. 9). In other words *E. penkillensis* is relatively wider, but less curved, than the contemporary Scandinavian species.

The form described by Davidson (1868, 1873) ; as *L. transversalis*, which occurs in such numbers in the Pentland Hills may also be referred to *penkillensis*. Lamont (1947 : 200) discusses the identification of this form without conclusion apart from suggesting that a number of different forms may exist. Collections, as well as the specimens in the Davidson collection, from three Pentland localities indicate that only one species is present, and that this falls within the range of *penkillensis* from both Scotland and Shropshire. The age of the Pentland beds is very probably *crenulata* Zone of the Telychian, although there is a slight possibility that they could extend into the lowermost Wenlock.

The lower part of the range of *E. penkillensis* is not fully documented. Forms from the Middle Llandovery (Idwian) of the Llandovery area may be referred to the species, as can the roughly contemporary population at Newlands, Girvan. Nothing earlier is yet known, but the range of variability of all species of *Eoplectodonta* is such that some specimens of *E. penkillensis* are similar to small forms of *E. duplicata*, and there seems to be no need to look further than the latter species for a possible ancestor.

Eoplectodonta transversalis (Wahlenberg)

(Plate 12, figs. 1–13)

1819 *Anomites transversalis* Wahlenberg : 64.
1828 *Leptaena transversalis* (Wahlenberg) Dalman : 109, pl. 1, fig 4.
non 1871 *Leptaena transversalis* (Wahlenberg) ; Davidson : 318, pl. 48, figs. 1–9.
? 1894 *Plectambonites transversalis* (Dalman) Hall & Clarke ; 295, pl. 15, figs. 34–6.
non 1916 *Plectambonites transversalis* (Wahlenberg) ; Holtedahl : 83, pl. 15, figs. 1–4.
non 1917 *Plectambonites transversalis* (Dalman) ; Reed : 886, pl. 15, figs. 35, 36.
non 1928 *Sowerbyella transversalis* (Davidson), pars [Wahl. ?] Jones : 448, pl. 23, fig. 23, pl. 24, fig. 1.
1929 *Plectodonta transversalis* (Dalman) Kozlowski : 113.
1967 *Ygera transversalis* (Wahlenberg) Havlíček : 58.

Diagnosis. Smaller *Eoplectodonta* with a lower length/width ratio, a less incurved umbo and larger interarea, and finer brachial valve septa than most other species.

Description. *Exterior.* Pedicle valve convex, maximum convexity near valve apex and decreasing anteriorly, with brachial valve concave. Pedicle umbo prominent, pedicle valve very enrolled over hinge line, so that interarea more visible when viewed from above as compared with other species (see Plate 12, figs. 3, 9 and 11 ; compare these with the more enrolled pedicle valve and smaller interarea of *Eoplectodonta duvalii* on the same plate, fig. 16). Outline semicircular to semi-oval, with length often approaching width. However small specimens often quite alate ; the growth sequence is first one of increasing width and finally one of increasing length

(shown by the growth lines on the neotype, Plate 12, figs. 1–3). Size of adult specimens small for *Eoplectodonta* ; maximum width 14 mm. in a population of more than 300 specimens. Ornament unequally parvicostellate with 12–30 larger ribs (depending mainly on length of specimen) some of which arise by intercalation anteriorly (Plate 12, fig. 11). Between 5 and 11 fine costellae between each large rib, some so fine as to to be almost invisible, appearing merely as rows of pseudopunctae through the translucent shell. Growth lines often prominent over valve surface, occasionally showing tendency to be lamellar. Small rugae seen only rarely, confined to the area

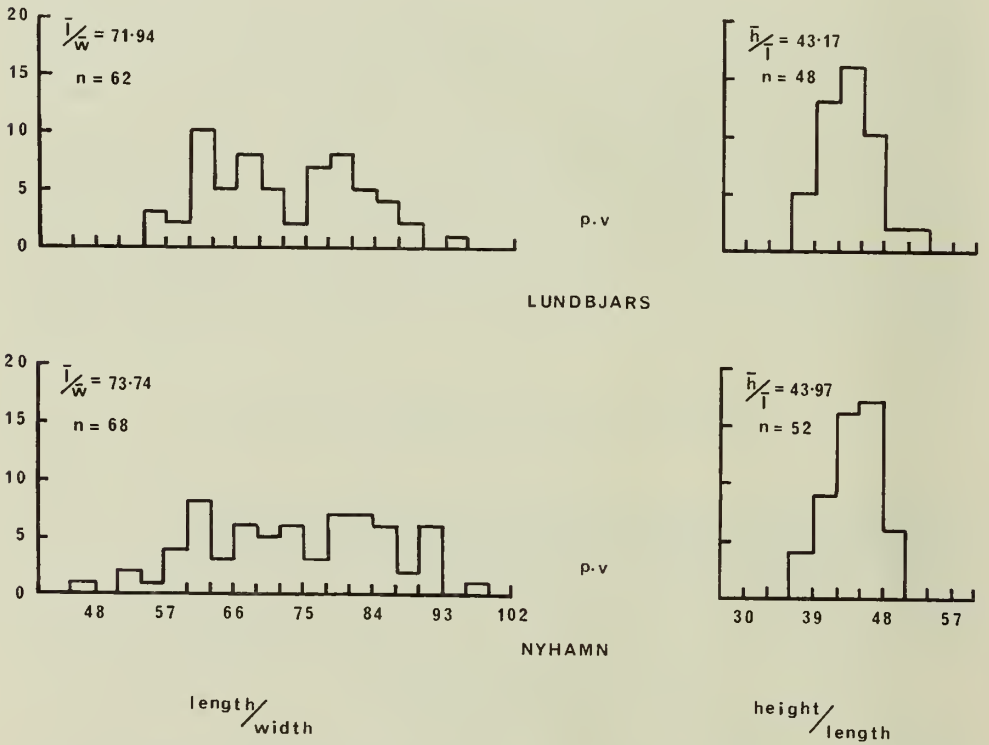

Fig. 8. Variation of *Eoplectodonta transversalis* in two populations from the Lower Visby Marl (Telychian) of Gotland, Sweden. Abbreviations as in Text-fig. 7. Bottom axis percentages with 3% class intervals.

near the alae. Interareas relatively large for the genus, at a shallow angle to each other. Oblique denticle growth tracks can be seen through the translucent shell. Delthyrium with sides sometimes straight and sometimes curved, diverging between 90 and 105 degrees. On either side are a pair of almost vestigial deltidial plates. Small discrete chilidial plates between which can be seen the cardinal process shaft and sometimes the two lateral processes (Text-fig. 3c). Small apical foramen occasionally seen, but often plugged by calcite.

Pedicle Valve Interior. Hinge line denticulate from between half and nearly all its length, with large denticles set oblique (Plate 12, figs. 10, 12, 13). Denticle length often irregular ; they protrude anteriorly slightly more on each side of the delthyrium, analagous with the stropheodontid composite plate. Dental plates fused to the edge of the delthyrum, flaring anterolaterally, continuing as muscle bounding ridges dying out anteriorly to fuse with the valve floor (seen in oblique view in Plate 12 fig. 12). Short median septum in the posterior part of valve, bifurcating, then merging with valve floor. Muscle field is similar to *Eoplectodonta duplicata*, described above in section on morphology (text-fig. 2). Vascular system (Plate 12 fig. 10) consisting of two main canals bifurcating near anterior margin, the two branches giving off many secondary branches. Valve interior is highly papillate, more than other species of *Eoplectodonta*, apart from the smooth central field.

Brachial Valve Interior. Hinge line has small fossettes to accommodate pedicle valve denticles. Cardinal process prominent, apparently fused posteriorly to the pair of chilidial plates. Pit in front of the cardinal process very deep, extending nearly to the valve exterior under the apical node. Thus the cardinal process appears a hollow structure, in contrast to the more massive deposits of secondary calcite found in *E. duvalii* (compare Plate 12 fig. 4 with Plate 12 fig. 14). Clavicular plates flaring anterolaterally, relatively short and spikey. Median septum variably developed ; never as strong as side septa, sometimes only developed anteriorly (Plate 12 fig. 4), sometimes for most of the valve length (Plate 12 fig. 7). Inner side septa prominent, nearly reaching pedicle valve when the valves are shut, apart from posteriorly where there is a well developed geniculation to accommodate the body cavity. These septa usually thicker at top than base, but tops not as thick as those of outer side septa in adults. Outer side septa smaller than inner in young, but grow larger and often end up larger than inner side septa. The relationship of the two pairs of septa also varies ; in some specimens (Plate 12 fig. 7) the two pairs join anteriorly, in other specimens (Plate 12 fig. 6) the inner pair wrap over the top of the outer pair, whilst in yet other specimens (Plate 12 fig. 4) the inner side septa curve round anteriorly becoming continuous with the bema enclosing the outer side septa. Bema emerges from behind clavicular plates in an anterolateral direction curving round first directly anteriorly, then antero-medianly, sometimes to die out, at other times merging with inner side septa. Bema sometimes more elevated off valve floor than other species of *Eoplectodonta*. Vascular canal system not well developed. Papillae very coarse (outside the muscle field) compared with *Eoplectodonta penkillensis*.

Type specimens. The original material of Wahlenberg has been lost, probably by incorporation into large poorly labelled general collections (Dr. A. Martinsson has kindly searched the collection at Uppsala on my behalf). The originals of Dalman's figures are also unidentifiable in the Dalman Collection at Naturhistoriska Riksmuseum, Stockholm. Dalman's figures are stylised views of complete specimens, whibh are in any case difficult to identify with particular individuals. The material in the Riksmuseet is poorly localized, except to identify the original horizon of *transversalis* as the Lower Visby Marl of Gotland. Thus I have selected a neotype from my own collection and given it to Naturhistoriska Riksmuseum, registered

number RMS Br 102394 (Plate 12, figs. 1–3). The locality is Lower Visby Marl, freshly weathering out at base of cliff at beach exposure 1 km W. of Lundbjars, 800 m. N of Nyhamn, Gotland. Swedish Grid reference CK/465 062.

Localities and material. Lower Visby Marl (Upper Telychian), Gotland, Sweden.

(i) marl weathering out from base of cliff, 1 km west of Lundbjars, and 800 m north of Nyhamn. Swedish Grid Ref. CK/465 062. (Plate 12, figs. 1–5, 8, 11–13) (RMS Br 102394, BB 32420–4, BB 32857–61 etc.).

(ii) marl weathering out of foreshore exposure, 200 m north of Nyhamn. Swedish Grid Ref. CK/463 055. (Plate 12, figs. 6, 7, 9, 10) (BB 32425–8 etc.).

(iii) other localities on NW coast of Gotland where the valves may be found loose on the foreshore include Norderstrand, Snäckgärdsbaden and Irevik.

Dimensions (in mm.)

	l.	w.	h.
All specimens from Lundbjars			
RMS Br 102394, conjoined valves, neotype (Plate 12, figs. 1–3)	10·6	approx. 13	4·7
BB 32422, conjoined valves (Plate 12, fig. 11)	10·5	13·4	4·7
BB 32857, conjoined valves	11·2	11·8	5·0
BB 32858, conjoined valves	7·4	10·9	3·2
BB 32859, conjoined valves	6·5	9·2	2·5
BB 32860, conjoined valves	6·5	10·9	2·9
BB 32861, conjoined valves	5·7	8·1	2·2

Discussion. With the doubtful exception of some figures of American material from the Niagara Group at Lockport by Hall & Clarke (1894), *Eoplectodonta transversalis* has not been authentically illustrated since the classic paper by Dalman (1828), who provided the first pictures of the species which Wahlenberg had erected without figures in 1819.

There can be no doubt from Dalman's figures of *transversalis* that they represent the *Eoplectodonta* which may be found in such numbers in the lower Visby Marl of Gotland, Sweden. This form has a significantly lower and more constant length-width ratio than its contemporary British species *penkillensis* (Text-fig. 9), caused not so much by initial differences as by differential growth along the length axis rather than the width.

The species of *Eoplectodonta* from Gotland are in some need of review. In his many admirable stratigraphical works, culminating in his guide to the International Geological Congress (1960), Hede lists the following (all of which he referred to *Plectodonta*). " *transversalis* (Dalman) " from the Lower Visby Marl ; "*transversalis lata* (Jones) " from the Upper Visby Marl and Slite Group and " cf. *duvali* (Davidson) " from the Högklint Beds. Hede is correct in the separation of the different forms which occur on Gotland, but was without the type English material for reference. It is now known that in England *lata* is a junior synonym of *duvalii* (see below). However there is in the Upper Visby Marl of Gotland a very large and wide form of *Eoplectodonta* which does not seem to be found elsewhere. This form (Plate 13,

fig. 1) is relatively rare, and at such rich localities as Kneippbyn, I was not able to procure a good enough sample to warrant full description. There is such a sample in the Naturhistoriska Riksmuseum, Stockholm (Br 31330–96), but it is without locality. There is no doubt that this material is specifically distinct from *transversalis*, but its relationship with genuine *duvalii* populations is less easy to estimate. English *duvalii* is not so large (some of the Gotland material is over 28 mm. wide).

FIG. 9. The pedicle valves of *Eoplectodonta transversalis* from Gotland compared with *E. penkillensis* from Shropshire. Data summed from Text-figs. 7 and 8. Bottom axis percentages with 3% class intervals.

The extra size is made up, however, not by an overall increase, but in a larger proportion of shell material outside the bema, so that the central septal region remains similar in size to large *duvalii* and thus appears small in relation to the rest of the shell. To name this form would be premature on the evidence at present available ; perhaps a new subspecies of *duvalii* would be most apt, hence the title of *Eoplectodonta* aff. *duvalii* to the figured specimen. What Hede refers to as *transversalis lata* from the Slite Beds (Plate 12, figs. 14–16) and as " cf. *duvali* " from the Högklint, may be referred to *Eoplectodonta duvalii sensu stricto*, described below.

Thus, although *transversalis* has probably been the most widely quoted sowerbyellid species, particularly by stratigraphers, it appears to be confined to one formation, the Lower Visby Marl of Gotland, of uppermost Llandovery (high Telychian) age. However it is possible that the species could also have occurred outside Europe.

Two large populations were recovered from existing outcrops on Gotland, at Lundbjars and Nyhamn. The fossil is also very common at many other places along the north-west coast of Gotland, but very often, as at the classic localities of " Visby " and " Norderstrand " the specimens form part of the beach shingle, weathered out from outcrops just below the wave line (there is almost no tide in that part of the Baltic).

Eoplectodonta duvalii (Davidson)

(Plate 12, figs. 14–16, Plate 13, figs. 3, 7, 10)

1847 *Leptaena transversalis* Dalman ; Davidson : 57, pl. 12, figs. 17–19.
1847 *Leptaena duvalii* Davidson : 58, pl. 12, figs. 20, 21.
1848 *Leptaena duvalii* Davidson ; Davidson : 317, pl. 3, fig. 7.
1848 *Leptaena transversalis* Dalman ; Davidson : 318, pl. 3, fig. 10.
1871 *Leptaena transversalis* Wahlenberg ; Davidson : 318 *pars*, pl. 48, figs. 1, 2, 4–6, ? figs. 7, 8, *non* figs. 3, 9.
non 1917 *Plectambonites transversalis* (Dalman) var. *duvali* (Davidson) Reed : 887, pl. 15, figs. 37–40.
1928 *Sowerbyella transversalis* (Davidson), *pars* [Wahl. ?] Jones 488, pl. 23, fig. 23, pl. 24, fig. 1.
1928 *Sowerbyella transversalis* var. *lata* Jones : 450, pl. 420 24, fig. 2.
1928 *Sowerbyella duvali* (Davidson) Jones : 451.
1954 *Sowerbyella transversalis* var. *lata* Jones : Nikiforova : 76, pl. 7, figs. 1–2.
1960 *Plectodonta transversalis lata* (Jones) Hede ; 73, 76.
1967 *Ygera lata* (Jones) Havlíček : 58.
1967 *Ygera transversalis* (Wahlenberg) Havlíček : 58 *pars*.

Diagnosis. Larger *Eoplectodonta* with up to 33 larger ribs, relatively small interareas and incurved pedicle umbo. A median septum is present in the brachial valve, but may be nearly obscured by secondary calcite.

Description. *Exterior.* Brachial valve concave and pedicle valve convex, but not usually so much as *E. transversalis*. Umbo fairly incurved and pedicle valve enrolled over hinge line. Shape alate and semicircular to semi-oval. Maximum width (23 mm in 50 specimens) at hinge line. Ornament unequally parvicostellate with a relatively large number of large ribs (33 counted in one specimen), with between 4 and 10 fine secondary costellae between each. Large undulations rare, although many specimens possess slight undulation (Plate 14 fig. 3). Growth lines sometimes seen, not as commonly or prominently as on *E. transversalis*. Small rugae often seen near the hinge line (Plate 13 fig. 10). Interareas set at an angle to each other which is sometimes acute and sometimes obtuse, but more of an angle than in *E. transversalis* and in general more than in *E. penkillensis*. Delthyrium open, the small deltidial plates of *E. penkillensis* apparently absent. In one population from the Buildwas Beds in the Davidson Collection (from Maw's washings—all registered B 1587) there is variation between forms with small discrete chilidial plates (as found in *duplicate*, *penkillensis* and *transversalis*) and forms in which the two plates have united to form an entire chilidium. Cardinal process, of central shaft and two lateral processes, visible from exterior through the open delthyrium (Text-fig. 3d and e). Small apical foramen visible in some specimens, often plugged by calcite.

Pedicle Valve Interior. The material of this valve showing the interior is poor. Hinge line denticulate for half or more of its length. Small median septum confined to umbonal area, bifurcating anteriorly before merging with valve floor. No teeth, but small dental plates flare away antero-laterally before merging with valve floor at side of muscle field. Vascular system unknown ; valve interior often papillose except on muscle field.

Brachial Valve Interior. In contrast with the pedicle valve good material has been available. Hinge line has fossettes for half or more of its length, some specimens entirely denticulate. Cardinal process roughly the same plane as anterior commissure, jutting posteriorly of the hinge line. Cardinal process supported only from the sides, anterior of process is a deep hollow extending very nearly to valve exterior. Antero-laterally of cardinal process are flaring clavicular plates (Text-fig. 2, Plate 12, fig. 15), with rounded anterior ends, raised up from the valve floor in a mound except medianly where they merge together with the posterior ends of the inner side septa to form a central elevated area of secondary shell. Median septum usually present, but very weak, almost vestigial in larger specimens, obscured by the growth of inner side septa (Plate 12 fig. 14). Inner side septa with geniculation near the umbo, curving outwards from valve floor, ending nearly at floor of pedicle valve. Outer side septa straight at their bases, but variably curved higher up, at their posterior end outwards, at their anterior end inwards. Bema variably developed, curving round nearly meeting anterior septa in the petaloid field. Vascular system not known. Large papillae outside central field.

Holotype. B 13730 from a calcareous band in the Wenlock Shale of Walsall (Plate 13 fig. 10). The specimen was collected by Mr. Lewis, who gave it to Davidson before 1847.

Dimensions (in mm.)

	l.	w.	h.
B 13730, pedicle valve, holotype (Plate 13, fig. 10)	—	16·8	—
GSM 12697, conjoined valves (Plate 13, fig. 7)	13·4	21·5	6·3
BB 50420, conjoined valves	11·3	approx. 17	5·2
B 34846, conjoined valves	13·2	21·2	6·6
B 23171, conjoined valves	10·4	approx. 20	4·2
B 8915, conjoined valves	10·0	15·0	4·8

B 13730 and BB 50420 are from Wenlock Shales of Daw End, Walsall, GSM 12697 is from Buildwas Beds at Buildwas and the last three specimens are from the Wenlock Limestone of Dudley.

Discussion. *Eoplectodonta duvalii* has been constantly misidentified. Davidson (1847) erected the species on a specimen which has its anterior part concealed by matrix (Plate 13 fig. 10). Thus it has the appearance of being a very transverse form in Davidson's original drawing—a drawing which was repeated both in his French paper (1848) and also in his much-used monograph (1871, pl. 48, fig. 5). As a result the name *transversalis* from Gotland was used for the common *Eoplectodonta* found in the Wenlock of England and elsewhere. Jones (1928 : 448) was at the disadvantage of not having much Swedish material and followed Davidson's mistaken interpretation of *transversalis*. Jones also erected the variety *lata* for specimens of larger size and smaller length/width ratio. However he states (1928 : 450) that " these characters [of *lata*] have been observed in forms from many localities, where they occur in association with normal types ". The holotype of Jones's variety (GSM 12697, Plate 13, fig. 7) although it is a large specimen, has a normal

length/width ratio of 62%, falling within the variation of *E. duvalii* ; thus Jones's variety is here placed into synonomy and not treated as a valid subspecies.

A fuller treatment of the distribution of *E. duvalii* in England, together with locality details, will be given by Dr. M. G. Bassett in his forthcoming monograph.

As discussed above, there is an *Eoplectodonta* in the Upper Visby Marl of Gotland (Plate 13 fig. 1) which may be a subspecies of *duvalii*, but it has not been formally described here. *E. duvalii* s.s. also occurs in Gotland, in particular the Slite Marl (Plate 12 figs. 14–16).

The relationship between *E duvalii* and *E. sowerbyana* (Barrande), from the Wenlock Litěn Beds of Bohemia is difficult to assess, particularly since the Czech material occurs only as moulds in a tuff, so that ornamental details are obscure, though the vascular system is well developed (Havlíček 1967, pl. 7). Certainly the relative emphasis of internal details (Plate 13, figs. 2, 4–6, 8, 9) differs from typical specimens of *E. duvalii*, but the full range of variation of the latter is not yet definitively known, and the taxonomic identity of *sowerbyana* remains obscure, although the species may definitely be included within *Eoplectodonta*.

The form from the Kitaigorod Formation of Podolia, described by Nikiforova (1954) may also be ascribed to *Eoplectodonta duvalii* (Plate 13 fig. 3). From material collected by Dr. P. T. Warren and Dr. J. Shirley in 1968, this formation may be referred to the Wenlock Series, rather than the Llandovery. Previous support for a Llandovery age is the record of *Pentamerus oblongus* (J. de C. Sowerby), confined to Llandovery rocks of Lower Telychian (C_4) age or older. However the large pentamerids present are not *P. oblongus* but a species of *Pentamerus* which continues throughout the Wenlock, occurring rarely even in the Wenlock Limestone of Dudley (BB 31279).

Ygerodiscus Havlíček 1967

1967 *Ygerodiscus* Havlíček : 62.

Type species. *Leptaena transversalis* var. *undulata* Salter 1848.

Discussion. As mentioned in the discussion of the subfamily, populations of plectambonitaceans had a variable tendency for their shells to become buckled. Often this tendency was phenotypic, but in the Lower Silurian there are a group of populations, descendants of *Eoplectodonta*, in which buckling is invariably present, and which are also specifically distinct from contemporary unbuckled *Eoplectodonta*. Havlíček (1967) has coined the generic term of *Ygerodiscus* for these forms, and this will also be used here, despite the possibility that these species should be included in *Eoplectodonta*. One of the most compelling reasons for the distinct treatment of the two genera was the discovery, in the population of *Ygerodiscus undulatus* from Meifod, of common small *Ygerodiscus* associated with a few large specimens of *Eoplectodonta*, indicating that by the Middle Llandovery the differences had probably become truly genetic.

The following species are attributed to the genus:—

Leptaena transversalis var. *undulata* Salter 1848 (synonyms *Sowerbyella undulata*

var. *maccoyi* Jones 1928. *Sowerbyella plicata* Jones 1928, and *Sowerbyella compressa* Jones 1928).

Ygerodiscus novemcostatus Havlíček 1967, Wenlock Liteň Formation of Bohemia.

Plectambonites striatacostatus Twenhofel 1928, Llandovery Gun River and Jupiter Formations of Anticosti.

Plectodonta propinqua Rybnikova 1967, Llandovery boreholes in Latvia.

In addition *Leptaena segmentum* var. *cornuta* Davidson 1883 is doubtfully included within *Ygerodiscus* (see below).

Ygerodiscus undulatus (Salter)

(Plate 14, figs. 3–12, Plate 15, figs. 1–12)

1848 *Leptaena transversalis* var. *undulata* Salter *in* Phillips : 372.
1852 *Leptaena quinquecostata* (M'Coy) pl. iH, figs. 30, 31, 31a.
1866 *Leptaena transversalis* (Dalman) var. *undulata* Salter ; Salter *in* Ramsay : 267.
1871 *Leptaena transversalis* (Wahlenberg) ; Davidson : 320, *pars*, *non* pl. 48, figs. 1–9.
1873 *Leptaena transversalis* (Dalman) var. *undulata* Salter; Salter : 64, 82.
1928 *Sowerbyella undulata* (Salter) Jones : 452 *pars*, pl. 24, fig. 3, *non* figs. 4–6.
1928 *Sowerbyella undulata* var. *maccoyi* Jones : 457, pl. 24, fig. 7.
1928 *Sowerbyella plicata* Jones : 459, pl. 24, figs. 10, 11.
1928 *Sowerbyella compressa* Jones : 460, pl. 24, figs. 12, 13.
1951 *Sowerbyella undulata* (Salter) ; Williams : 130.
1951 *Sowerbyella undulata maccoyi* Jones ; Williams : 130.
1967 *Sowerbyella undulata* (Salter) : Rybnikova : 187, pl. 18, figs. 11–13.
1967 *Ygerodiscus undulatus* (Salter) Havlíček : 62.
1967 *Ygerodiscus undulatus maccoyi* (Jones) Havlíček : 62.
1967 *Ygerodiscus compressus* (Jones) Havlíček : 62.
1967 *Ygerodiscus plicatus* (Jones) Havlíček : 62.

Diagnosis. *Ygerodiscus* with interior arrangement very close to *Eoplectodonta*, number and strength of plicae variable. Small size, with average width of about 10 mm.

Description. *Exterior.* Pedicle valve convex, often more than a semicircle in profile, with concave brachial valve. Incurvature of umbo and enrollment of pedicle valve over hinge line variable but often strong. Outline semicircular and alate. Size is small for family—maximum width of 16·1 mm. in 140 specimens. Ornament unequally parvicostellate with between 7 and 18 larger ribs, between each from 6 to 12 very fine costellae. Coincident with the 5 to 12 central large ribs is a series of undulations, with the primary rib at the crest of the undulation in the pedicle valve and in the trough in the brachial valve. Two small undulations variably occurring on either side of the median rib in both valves (Plate 15, fig. 2), dying away anteriorly just past the umbo, these are also diagnostic of *Eoplectodonta duplicata*. Growth lines occasionally seen (Plate 14, fig. 4). Small rugae sometimes developed, confined to hinge area and alae. Interarea of the pedicle valve wider than brachial valve, the interareas at an obtuse angle. Delthyrium has pair of small, discrete, triangular chilidial plates. Shaft of the cardinal process visible along its length, the two lateral processes seen above the chilidial plates. Small apical foramen occasionally seen, but usually plugged by calcite.

Pedicle Valve Interior. Hinge line denticulate from between a quarter and three-

quarters of its length. No teeth, but small pair of antero-laterally directed dental plates at a continuation of angle of delthyrium sides. Plates die out quickly anteriorly. Muscle system similar to *Eoplectodonta*. Small thin median septum confined to umbonal area bifurcating before merging with the valve floor. Vascular markings often well developed ; two main trunks running anteriorly from under the muscle field some way to the valve margin (plate 15, figs. 1, 7, 8), before dividing laterally. Prominent papillae often developed near alae and round anterior valve margin (Plate 15, fig. 8).

Brachial Valve Interior. Hinge line fossettes correspond with pedicle valve denticles. Cardinal process trifid, supported from sides, forming the posterior wall to hollow extending nearly to valve exterior. Prominent clavicular plates, varying within one population from blade-like to squat and triangular. Median septum well developed, running from near the valve umbo for about three-quarters the length of the valve. Inner side septa prominent, their tops geniculate in profile near the valve umbo. Sometimes these septa split into two parts anteriorly (Plate 14, figs. 6, 11), but groove between these two parts does not get near the valve floor. Outer side septa present, but not so strong, and as little as half length of inner side septa. Bema usually well developed, sometimes raised much off the valve floor. Muscle system similar to *Eoplectodonta*. Vascular system poorly known. Very coarse papillae sometimes present, particularly towards valve ears and anterior margin (Plate 14, fig. 6).

Type specimen. The lectotype, chosen by Jones (1928 : 455–6) is SMA 11307 (previously registered as a/198), a mould of the exterior of a brachial valve (Plate 15, fig. 5). It is one of M'Coy's original specimens, and comes from the " Bala Schists of Mathyrafal ", and has the label " Math " stuck to it in M'Coy's writing. The locality is discussed below.

Localities and material. V_2c horizon (late Rhuddanian or Idwian), bank of River Banwy, near Meifod, Montgomeryshire, Wales. Grid Ref. SJ/1327 1057 (Plate 15, figs. 1, 4, 7–9), figs. 2 and 5 come from this or a very similar locality) (SMA 11307–8, BB 31669, BB 31903–28).

Rosemarket Beds (Idwian or early Fronian), old quarry 700 yards S of Bullford, near Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/9218 0980. (Plate 14, figs. 3–9, 11, Plate 15, figs. 6, 10–12) (GSM 37560–3, GSM OJT 1000–1104, BB 32081–4 etc.).

C_1 Beds (Fronian), " near footbridge " (now disappeared) over River Sefin, south of Lletty'rhyddod, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/7418 2817 (Plate 14, figs. 10, 12) (BB 32417 etc.).

B Beds (Idwian) exposure on forestry track, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/8344 3726. (Plate 15, fig. 3)(BB 32109 etc.).

B_3 Beds (Idwian), small disused quarry by roadside, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/760 309 (BB 32085–7, 32094 etc.).

Williams (1951 : 130) lists the species as occurring in all horizons in the Llandovery area between A_2 and C_{2-3} beds inclusive. I would treat at least the A_2 and A_3 populations as variants of *Eoplectodonta duplicata*.

DIMENSIONS (in mm.)

		l.	w.
All specimens from Meifod			
SMA 11307 brachial valve exterior, lectotype	(Plate 15, fig. 5)	5·9	16·1
SMA 11308 ,, ,, ,,	(Plate 15, fig. 2)	6·0	approx. 12
BB 31928 ,, ,, ,,		4·5	11·0
BB 31904 pedicle valve interior		4·8	approx. 12
BB 31909 ,, ,, ,,		3·5	7·3
BB 31913 ,, ,, ,,		5·5	13·2
BB 31910 ,, ,, ,,		7·3	10·0

DISCUSSION. M'Coy figured the holotype (1852 pl. iH, fig. 30) as "*Leptaena quinquecostata* (M'Coy), transverse variety with additional lateral ridges". This figure was quoted by Salter (*in* Ramsay 1866) as *Leptaena transversalis* Dalman var. *undulata* Salter, and the individual specimen appears in Salter's type catalogue of 1873. In addition M'Coy figured (1852, pl. iH, figs. 31, 31a) a second specimen (SMA 11308) from the same locality, which was subsequently chosen by Jones (1928 : 457) as the type of his new variety *maccoyi*. The differences between the two specimens, both natural casts of externals of brachial valves, are due to normal variation at the locality. Mathyrafal is the name of a ruined castle (spelt Mathrafal on Ordnance Survey maps) situated on the land of Upper Hall Farm, 2 miles S.W. of Meifod in Montgomeryshire. M'Coy's locality was almost certainly in the section of the Llandovery exposed in the bank of the River Banwy, about 200 yards south of the castle site. A comparative collection which contained *Ygerodiscus undulatus* was made from the river bank at Grid Ref. SJ/1327 1057 which must be at, or very near, the type locality. This area has been described by King, who gives a geological section along the river bank (1928 : fig. 2). The type locality lies in King's V_2c beds which he considered to be Middle Llandovery or even Low Upper Llandovery in age. However, recent work by Dr. J. T. Temple (1970, in press), as well as collecting by the present author, indicates that this horizon is at least partly late Lower Llandovery in age, although the Middle Llandovery may also be present.

The type specimens of *Sowerbyella plicata* and *Sowerbyella compressa* both come from the same small quarry in Pembrokeshire, and an examination and measurement of O. T. Jones's original collection, leaves no doubt that the few specimens which he labelled *compressa* are oblique to the bedding plane, and distorted specimens of *plicata*.

The age of this locality requires discussion. The Rosemarket Beds outcrop as a strip just over nine miles long, to the south of, and unconformable upon, the Pre-Cambrian Johnston Series in Pembrokeshire, Wales. The Geological Survey (Strahan *et al.* 1914, Cantrill *et al.* 1916) mapped the beds as a lower conglomerate and an upper mudstone, more than 1000 feet thick. The type locality of *plicata* is on the Milford Haven Sheet, a small farm quarry now filled with refuse. However loose blocks within ten yards of the quarry have an identical lithology, a light brown fine sandstone, to that of the type material. (There are no glacial deposits in the immediate area.) The collection contained the following brachiopods :—*Pentamerus*

oblongus (J. de C. Sowerby), *Ygerodiscus " plicatus* (Jones) ", *Coolinia* aff. *applanata* (Salter), *Clorinda* sp., *Protatrypa* sp. and an indeterminable rhynchonellid. There were also the corals *Halysites* sp., and *" Petraia "* sp. and at least two species of decalcified polyzoa. *Pentamerus* is unknown before the Middle Llandovery, but does not reach its acme until the Fronian, before evolving into *Pentameroides* in the Telychian. *Protatrypa* evolved into *Atrypa* during the Fronian. Subsequently a re-examination of the Geological Survey collection from the locality revealed a graptolite hitherto overlooked. Although poorly preserved, the specimen [on GSM OTJ 1045] has been kindly identified by Dr. P. Toghill as probably *Glyptograptus tamariscus*, unidentifiable as to subspecies, but one of the narrow forms which occur between the *cyphus* and *sedgwickii*-Zones inclusive. Thus the type locality of *Ygerodiscus plicatus* may be taken to be of Idwian (Middle Llandovery) or perhaps early Fronian age. The area as a whole needs revision ; for example a collection from the old quarry at the south end of the lane leading from Great Nash [Grid Ref. SM/9750 0949], mapped as Rosemarket Beds (Strahan *et al.*, 1914 : 112), in fact yields an Ashgill fauna.

Thus there are two nominal species of *Ygerodiscus* (having eliminated *maccoyi* and *compressa*) viz. *undulatus*, from the late Rhuddanian or Idwian of Meifod, and *plicatus* from the Idwian or early Fronian of Pembrokeshire. There is an age gap of between nought and about seven million years depending on the correlation chosen, and a geographical separation of a hundred miles. Half way between these localities, at Llandovery itself, occur several populations of *Ygerodiscus* which can be unequivocally dated as being Idwian in age (see localities above). These populations confirm the view that the two forms are so close that any separation would be invidious. Thus *plicatus* is treated here as a junior synonym of *undulatus*.

The species is just as denticulate as *Eoplectodonta*. Jones (1928 : 456) suspected the presence of denticles in *undulatus*, and illustrated them in *plicatus* and *compressus*, but neither Kozlowski (1929) nor Williams (1951) referred the species to *Plectodonta* ; Havlíček (1967) referred all four names to *Ygerodiscus*.

As discussed earlier under the genus, *Ygerodiscus undulatus* probably evolved from end members of *Eoplectodonta duplicata* populations at some time during the late Rhuddanian. That the two became genetically distinct quite quickly is indicated by the presence in the collection from Meifod of numerous smallish *Y. undulatus* intimately associated with a few larger *E. duplicata*, without forms connecting the two groups.

? *Ygerodiscus cornutus* (Davidson)

(Plate 13, figs. 11, 12, Plate 14, figs. 1, 2)

1883 *Leptaena segmentum* var. *cornuta* Davidson : 166, pl. 12, figs. 1–3.
1928 *Sowerbyella cornuta* (Davidson) Jones : 461.
1967 *Ygerodiscus cornutus* (Davidson) Havlíček : 62.

MATERIAL. Four specimens in the Davidson Collection, from Middle Wenlock Shales (Coalbrookdale Beds), half a mile west of Buildwas Abbey, Shropshire,

England, all registered B 5828. A lectotype is selected here (Plate 13, figs. 11, 12), and has been re-registered BB 32416.

Measurements (in mm.)

	l.	w.
BB 32416, conjoined valves, lectotype	5·4	11·2
B 5828, conjoined valves	4·5	8·9

Discussion. All four specimens consist of conjoined valves, and their internal details are largely unknown. However, when viewed through water, denticles are visible along the hinge line, and the species is tentatively referred to *Ygerodiscus*, as suggested by Havlíček (1967), since the valves are to some extent undulate. It is however possible that it should belong in *Eoplectodonta*, but the species is distinct from contemporary sowerbyellids in its different outline, which is trapezoidal, with antero-lateral pojections. ?*Ygerodiscus cornutus* is rare ; only four specimens were collected from more than a ton of the shale washings processed by Maw and Davidson, in other respects richly fossiliferous.

Anisopleurella Cooper 1956

1956 *Anisopleurella* Cooper : 804.
1965 *Anisopleurella* Cooper ; Williams : H380.

Type species. *Anisopleurella tricostellata* Cooper 1956.

Discussion. The genus is known by the two Porterfield species originally described by Cooper, *A. tricostellata* and *A. inaequistriata*, and by *A. balclatchiensis* (Reed 1917) from the contemporary Balclatchie Mudstones of Scotland (Williams 1962 : 185). In addition Cooper (1956 : 805) attributed *Orthis quinquecostata* M'Coy 1846 to *Anisopleurella* and Williams (1962 : 187) attributed *Sowerbyella multiseptata* Williams 1955. Havlíček (1967 : 55) described *A. ovalifera* from the Ashgill of Bohemia and also attributed *Sowerbyella gracilis* Jones to the genus without redescription. *A. gracilis* is the only post-Ordovician species yet recorded.

Dr. G. A. Cooper has kindly sent over on exchange topotype specimens of *Anisopleurella tricostellata*, (BB 32855–6) from the Pratt Ferry Formation (basal Caradoc) of Alabama, for comparison with *A. gracilis*.

Anisopleurella gracilis (Jones)

(Plate 16, figs. 1–9)

1914 *Plectambonites* cf. *quinquecostatus* (M'Coy) ; Jones *in* Strahan *et al.* : 80 *et seq.*
1928 *Sowerbyella gracilis* Jones : 472, pl. 24, figs. 21–25.
1967 *Anisopleurella gracilis* (Jones) Havlíček : 55.

Diagnosis. Small *Anisopleurella* with thin shell curved socket plates and petaloid muscle field. Few structures in the pedicle valve.

Description. Owing to the thinness of the shell, the specimens have all suffered crushing, in most cases severe, during the compaction of the fine shale in which they

are found. Thus details of the following description will doubtless be amplified if good uncrushed material, especially with shell preserved, is later found.

Exterior. Brachial valve concave, pedicle valve convex. Outline semicircular and alate. Umbo usually incurved, and hinge line enrolled. Small node at the otherwise concave umbo of the brachial valve. Maximum width at hinge line. Ornament unequally parvicostellate, with three (Plate 16, fig. 7) or more larger ribs and large number of small parvicostellae between them. In some shells, particularly those with many primary ribs (as many as 20) the distinction between the strength of the two types of ribs breaks down, and there are more or less equally parvicostellate areas. Growth lines not usually seen. Small undulations sometimes present. Faint small rugae occasionally laterally. Interarea difficult to see clearly on account of crushing, delthyrium possibly open, but a small deltidium or perhaps a pair of small deltidial plates is suspected. Trifid cardinal process visible from exterior ; chilidial structures uncertain. Apical foramen not seen. Very prominent " ribs " seen on many exteriors (Plate 16, figs. 1, 3, 4, 7, 8) due to post-mortem crushing, when the relatively stout brachial valve septa got pushed through the thin shell of both valves.

Pedicle Valve Interior. In a few pedicle valves from the Cartlett Beds there appear to be very faint crenulations on the hinge line ; however they are too faint to be called denticles and are absent from most specimens, whose hinge lines seem quite smooth. No teeth, but weak dental plates, merging with valve floor a short distance anteriorly. No median septum ; no muscle bounding ridges. No trace of the muscle field or vascular markings. Shell often covered with papillae outside the smooth central area, but papillae size small.

Brachial Valve Interior. Clavicular plates very thin, diverging widely, curving right round parallel to, and trending posteriorly towards, the hinge line. Cardinal process small for a plectambonitacean. Median septum approximately half-way to anterior margin. Inner side septa thin, running anteriorly to about the same distance as the median septum. Outer side septa strong, starting posteriorly only just anterior of the cardinal process, becoming wider anteriorly, but usually not as far as inner side septa. Bema curving round anteriorly from beneath clavicular plates, with valve floor antero-laterally of outer side septa, giving a bi-petaloid central field. Muscle system and vascular system not seen. Small papillae common outside central field.

Type specimen. Holotype (by original designation of Jones 1928, caption to Plate 24, fig. 21) GSM 37554, an external mould of a pedicle valve from the Cartlett Beds, south side of railway cutting, 650 yards SW of Priory Mill, SE of Haverfordwest, Pembrokeshire, Wales.

Dimensions (in mm.)

	l.	w.
GSM 37554, mould of both valves, holotype (Plate 16, fig. 1)	5·0	approx. 9
GSM 37551, external mould of pedicle valve (Pl. 16, figs. 4, 7)	4·2	7·9

	l.	w.
BB 32043, external mould of brachial valve	5·1	9·5
BB 32028, external mould of brachial valve	2·6	approx. 4
BB 31996, external mould of brachial valve	3·9	7·2
BB 32049, external mould of brachial valve	5·0	8·5

Discussion. This small species occurs commonly at only one general locality and horizon, near the base of the Silurian in Pembrokeshire. The actual type locality is now obscured by grass on the cutting, but a good collection (BB 31995–32054) was obtained in 1968 about 20 yards west of the type locality [Grid Ref. SM/9564 1458] from a patch cleared for a new telegraph pole : the specimens seem indistinguishable from those in the type collection (GSM OTJ 766–90).

Anisopleurella gracilis also occurs rarely in the upper part of the Rhuddanian at Meifod (Temple 1970, in press). Jones (1928 : 473) and Williams (1951 : 130) record the species from as high as C_1 in the Llandovery area, but the present author has not seen material from above the Lower Llandovery.

Subfamily **AEGIROMENINAE** Havlíček

Havlíček (1967) included the following genera within the Aegiromeninae :—

Aegiria Öpik 1933
Aegiromena Havlíček 1961
Aegironetes Havlíček 1967
Chonetoidea Jones 1928
Sentolunia Havlíček 1967
Sericoidea Lindström 1953

Havlíček noted two main differences between the two subfamilies of the Sowerbyellidae, firstly the Aegiromeninae have a " circular or cordate visceral field ", whilst in the Sowerbyellinae the field is " halved into two oval lobes ". Secondly, in the Sowerbyellinae " in the longitudinal axis of each of the two lobes, there is a septum which evidently served for the attachment of adductors. In Aegiromeninae, however, adductors were directly attached to the bottom of brachial valve " (1967 : 37–8).

Apart from rare specimens of *Aegiromena* itself, the only two of these genera recorded from the Silurian are *Aegiria* and *Chonetoidea*, which are reviewed below. Since *Chonetoidea* has been so widely quoted, the opportunity is taken to describe and figure the type species, *C. papillosa*, from the Ashgill of Pembrokeshire ; Reed's original description has remained unamended.

Aegiromena Havlíček 1961

? *Aegiromena* sp.

(Plate 16, figs. 13, 14)

Discussion. A single pedicle valve, from the Middle Llandovery, Idwian, of Newlands, in the Craighead Inlier, near Girvan, Ayrshire, Scotland, may be tenta-

tively referred to this genus. Havlíček (1967) has described several species of *Aegiromena* from the Bohemian Ordovician, including *A. ultima* from the Upper Ashgill (Marek & Havlíček 1967), and in addition a single species, *A. myrmido* (Barrande) from the Litěn Formation, of Wenlock age. The genus has never been recorded from the Llandovery (apart from Temple's record (1968) of " *Aegiromena* sp. nov. " from the very base of the Llandovery).

The internal mould of the pedicle valve is typical of the genus, but the corresponding external mould shows an unequally parvicostellate ornament with occasional strong, widely spaced costae similar to those seen on *Leangella scissa*. Thus the final attribution to *Aegiromena* seems best left with a query, as the ornament of plectambonitaceans is capable of a very high degree of variation.

MEASUREMENTS (in mm.)

	l.	w.
HML 9931 Internal mould of pedicle valve (Plate 16, figs. 13, 14)	3·5	approx. 7

Chonetoidea Jones 1928

1928 *Chonetoidea* Jones : 389.
1933 *Chonetoidea* Jones ; Öpik : 51.
1957 *Chonetoidea* Jones; Spjeldnaes : 104.
? 1960 *Chonetoidea* Jones ; Sokolskaya : 210.
1965 *Chonetoidea* Jones ; Williams : H383.
1967 *Chonetoidea* Jones ; Havlíček : 48.

Chonetoidea (type species *C. papillosa* (Reed 1905) from the Ashgill of Pembrokeshire) was erected by Jones in 1928 to cover all of what he knew of the subfamily. Five years later Öpik (1933) erected *Aegiria* (type species *A. norvegica* from the Llandovery of the Oslo region), and detailed the following differences between the two genera in the form of a table (1933 : 51), comparing *papillosa* and *garthensis*, referring the latter species to *Aegiria*. His table has been kindly translated by Dr. R. P. S. Jefferies as follows :—

papillosa (Jones 1928, pl. 25 fig. 21 and Reed 1905, pl. 23, fig. 13)	*garthensis* (Jones 1928, pl. 25, fig. 26)
Brachial lamellae scarcely indicated	Brachial lamellae strongly developed and sharply defined
Cardinal pit deep with clear borders	Cardinal pit scarcely indicated
Median septum weak, side septa present	Median septum large ; no trace of side septa

In fact both species show comparable brachial lamellae (termed the bema in this paper), although they are stronger in *garthensis*. The cardinal pit (i.e. the hollow area immediately anterior of the cardinal process) is, if anything, deeper in the second specimen of *garthensis* (GSM 50417–8) than in any specimen of *papillosa* ; unfortunately the illustrated holotype of *garthensis* is slightly damaged near the cardinal pit, so although Öpik's observation was justified on Jones' illustration, his statement is incorrect.

However Öpik's third point, on the distribution of structures within the brachial valve, is certainly important. *Chonetoidea papillosa* has a number of structures (Plate 17, fig. 1), some of which are no more than elongated papillae, whereas all the species of *Aegiria* have a pronounced median septum and very little trace of side septa, and this appears to be a character of generic difference. The indefinite structure of *C. papillosa* is shared by *C. iduna* Öpik 1933 and *C. virginica* Cooper 1956, though the latter species, and also *C. gamma* Spjeldnaes 1957, both have differentiated ornament, and are probably referable to *Sericoidea* (this was suggested for *virginica* by Williams 1962 : 189). On the other hand, Spjeldnaes (1957 : 105, fig. 24) illustrates another two species, *C. alpha* and *C. stoermeri*, as possessing well-defined median septa, as well as many small side septa round a bema. *C. stoermeri* is one of the earliest members of the group, coming from Zone 4a and 3, equivalent to Llandeilo in age. However *C. alpha* and *C. stoermeri* might perhaps be placed in *Aegiromena* ; but revision of Ordovician forms is out of place in the present work, sufficient to say that *Chonetoidea* and *Aegiria* will be kept distinct until a detailed analysis of Ordovician forms is available.

As far as is at present known, despite many records to the contrary, *Chonetoidea* does not occur in the Silurian.

The form illustrated as " *Chonetoidea simorini* M. Borrisiak in coll. " from the Middle Ordovician of Kazakhstan by Sokolskaya (1960, pl. 27, figs. 24, 25) does not look as though it ought to belong in *Chonetoidea*.

Chonetoidea papillosa (Reed)

(Plate 17, figs. 1–3)

1905 *Plectambonites papillosa* Reed : 451, pl. 23, figs. 13–15.
1914 *Plectambonites papillosus* Reed, Jones *in* Strahan *et al.* : 67.
1928 *Chonetoidea papillosa* (Reed) Jones : 498, pl. 25, figs. 20–24.
1965 *Chonetoidea papillosa* (Reed) ; Williams : H383, fig. 244, 3a–c.

Diagnosis. *Chonetoidea* with a large number of subequally parvicostellate ribs. Small thin median septum in brachial valve, with large number of small side septa surrounding a faint bema.

Description. *Exterior.* Pedicle valve convex, brachial valve concave. Lateral profile gently curved, without enrollment of hinge line or umbo. Outline semicircular, only slightly alate. Size small for the family (maximum width 7 mm. in the type sample of 20 specimens). Ornament of large number of more or less equal parvicostellae (Plate 17, fig. 3) ; apparently random ribs sometimes stand out as stronger, but there seems to be no pattern in their distribution. Undulations (except tectonic), rugae and growth lines absent. Interarea wide, with both valves in nearly the same plane. Small arched deltidium. Trifid cardinal process clearly visible ; no chilidial plates or chilidium. Small but prominent protegular node on brachial valve. Foramen very small not usually seen, but there is evidence from several pedicle internal moulds (SMA 30848 etc.) that it was probably functional.

Pedicle Valve Interior. Hinge line finely denticulate (best seen on SMA 30847 and

SMA 11313). Along inside of hingeline, appearing as nodes on internal moulds, there are also small pits, up to two on each side of the umbo, not present in all specimens. Small pair of teeth and dental supports, too slight to be termed dental plates, on each side of the pedicle chamber. Faint and short median septum immediately anterior of pedicle area. Muscle scars and vascular system too faint for detailed description. Papillae near alae and anterior margin, finer than in brachial valve. Shell very thin, allowing exterior ornament to be seen on valve interior.

Brachial Valve Interior. Fossettes, although presumably present to accommodate pedicle valve denticles, not seen with certainty. Strong socket plates whose angle of divergence varies from 80 to 130 degrees, sometimes straight, sometimes curving round towards hinge line. In one specimen (SMA 11313) they split into two near their antero-lateral extremities. Between socket plates, anterior cardinal process, a hollow extending nearly to valve exterior. Thin median septum and many approximately equal-sized side septa, which may or may not be symmetrical. Faint bema in some specimens, absent in others. Sometimes small side septa cut through bema edge. Muscle field indistinct ; vascular system not seen. Papillae often quite large, grading into the small side septa.

Type specimen. Lectotype (here chosen) SMA 11311 (Plate 17, fig. 1), the original of Reed 1905, pl. 23, fig. 13. V. M. Turnbull Collection. Slade Beds (Ashgill), Upper Slade, Haverfordwest, Pembrokeshire, Wales.

Dimensions (in mm.)
All specimens from the type locality.

		w
SMA 11311 Brachial internal mould, lectotype (Plate 17 fig. 1)	2·5	5·9
SMA 30841 Pedicle external mould, (Plate 17, fig. 3)	3·1	5·3
SMA 30848 Conjoined valves	3·4	5·9
SMA 30844 Pedicle external mould	1·7	3·4
SMA 30845 Conjoined valves	3·2	4·8

Discussion. Havlíček (1967 : 49) described very small canals penetrating the pedicle valve interarea in *Chonetoidea radiatula* (Barrande) from the Ashgill Králův Dvůr shales of Bohemia. He notes that the fillings of these canals are only " exceptionally " preserved, and that on most of his specimens they are represented only by fine nodes on the interior of the mould of the pedicle valve. *Chonetoidea papillosa* also shows these nodes, although in no case in the type collection are any canals themselves preserved. The very fine denticulation on the hinge line, seen only on the larger specimens, has not previously been noted. Since they are contemporary, and do not appear to differ greatly from each other in material detail, it is possible that *C. papillosa*, *C. radiatula* and *C. tenerrima* Havlíček 1952 might in future be synonomised ; certainly the latter two species do not appear distinct, and occur in the same formation.

Aegiria Öpik 1933

1933 *Aegiria* Öpik : 55.
1952 *Aegiria* Öpik ; Havlíček : 399 etc *pars*.
1965 *Aegiria* Öpik ; Williams : H381.
1967 *Aegiria* Öpik ; Havlíček : 38.

Type species. *Aegiria norvegica* Öpik 1933, from the Middle Llandovery (Zone 6c) of Leangen, near Oslo, Norway.

Discussion. The relationships between *Chonetoidea* and *Aegiria* are discussed above. The line between the two genera (and *Sericoidea* with its unequal parvicostellae) is finely drawn when the complete range of variation is taken into account ; however Öpik's separation of the two genera is endorsed here.

So far as is known, *Aegiria* does not occur in the Ordovician. During the Silurian its occurrence is patchy ; in parts of the Llandovery and Ludlow it is present in swarms, in the Wenlock it is rare.

Silurian species assigned to *Aegiria* are as follows :—

Chonetoidea garthensis Jones 1928 : 500, pl. 25, figs. 25, 26, from the Lower Llandovery of Wales.

Leptaena grayi Davidson 1849 : 271, figs. 1, 1a, from the Wenlock Limestone of Dudley, England.

Aegiria norvegica Öpik 1933 : 55, pl. 10, figs. 1–5, pl. 11, figs. 3–5, from the Middle Llandovery of Leangen, near Oslo, Norway.

Chonetoidea sp. Borrissiak 1955 ; 50, pl. 9, figs. 9–13 from the Llandovery of the Chinghiz mountains of Kazakhstan, U.S.S.R.

Aegiria thomasi Talent 1965 : 24, pl. 6, figs. 1, 3, 5-7 from the Dargile Formation (Ludlow) of the Heathcote District, Victoria, Australia.

The following species may be referable to *Aegiria*, but require further investigation:

Plectambonites aequalis Teichert 1928 : 58, pl. 5, figs. 18–20, from the Middle to Upper Llandovery of Kiltsi, Estonia, U.S.S.R.

Plectodonta aknistensis Rybnikova 1967 : 188, pl. 19, figs. 1, 2, from Late Wenlock and Early Ludlow boreholes in Latvia, U.S.S.R.

Sowerbyella austrum Öpik 1953: 14, pl. 3, figs. 17, 18 from the Illaenus Band of the Wapentake Formation (Upper Llandovery), Heathcote District, Victoria, Australia.

Aegiria garthensis (Jones)

(Plate 17, figs. 4–7)

1928 *Chonetoidea garthensis* Jones : 500, pl. 25 figs. 25, 26.
1933 *Aegiria garthensis* (Jones) Öpik : 51 etc.

Diagnosis. Large *Aegiria* with many ribs, well-defined bema, and very divergent strong socket plates.

Description. The specimens originally described by Jones are still the only ones available, these are part and counterpart of two brachial valves, and thus the following description of the exterior is based only upon the brachial valve.

Exterior. Shape of brachial valve gently concave, with very slight median sulcus. Outline semicircular, and slightly alate. The two specimens known are rather large for the genus. Ornament of subequal parvicostellae (about 65 in number) of greater size in the central part of the valve than towards the ears. New ribs arise by intercalation and division. No rugae, undulations or growth lines are visible, but the parvicostellae are wavy and irregular in places in an apparently random fashion. Interarea fairly narrow, no chilidium or chilidial plates. Cardinal process visible from exterior, growing out posteriorly from hinge line. Small, poorly defined protegular node present.

Pedicle Valve Interior. Unknown.

Brachial Valve Interior. Hinge line apparently smooth. Strong pair of divergent socket plates, curving round to end up almost parallel with hinge line. Cardinal process and socket plates form posterior wall of small pit extending nearly to valve exterior. Immediately anterior of this there is the median septum, prominent and situated on top of the fold, so that all the anterior part of the valve interior appears divided into two parts. Bema is well defined ; no side septa. No muscle scars or vascular system seen. Exterior ornament seen on interior (outside the bema), but modified by papillae, which are slightly elongated and arranged in rows upon some of the exterior troughs providing an irregular pattern.

Type specimens. Holotype GSM 37589–90, a brachial valve (the part and counterpart are registered under two separate numbers), designated by Jones 1928, caption to pl. 25. Jones gives the locality as " Lower Llandovery (middle part) ; N. of Garth, Breconshire ". G. Andrew Collection.

Dimensions (in mm.)	l	w
GSM 37589–90, brachial valve, holotype (Pl. 17, figs. 5, 6)	2·8	approx. 8
GSM 50417–8, brachial valve (Pl. 17, figs. 4, 7)	3·4	8·8

Discussion. The locality given by Jones for the species is vague, and the species name was not used in the stratigraphical description of the Garth area (Andrew 1925) because it predates Jones's work. Jones' description is unhelpful since all the Llandovery of the Garth area is north of the village of Garth and the middle part of the Lower Llandovery (presumably Andrew's division Ab) has the largest outcrop of any division in the area. One of the specimens has λ 4 on it, but this cannot be correlated with Andrew's published localities since his locality 4 is in the Upper Bala. The only plectambonitids which Andrew cites from his division A b (1925 : 396) are *Plectambonites undulatus* and " a single specimen of *Plectambonites duplicatus* ", so that the locality of the type specimens of *Aegiria garthensis* must remain doubtful. Some collecting by the present author in the Garth area has not produced further material.

Öpik (1933 : 55, pl. 10 figs. 1–5, pl. 11, figs. 3–5) in his excellent description of *Aegiria norvegica*, compares it with *garthensis*, but many of his points of difference are debateable, and it is quite possible that the two species are synonymous. However, without knowledge of the pedicle valve of *garthensis* it would be premature to place *norvegica* into its synonymy.

Aegiria grayi (Davidson)
(Plate 17, figs. 8–14)

1849 *Leptaena grayi* Davidson : 271, figs. 1, 1a.
1852 *Leptaena* ? *minima* J. de C. Sowerby ; M'Coy : 235.
1871 *Chonetes* ? *minima* (J. de C. Sowerby) Davidson : 334, *pars*, pl. 49, figs. 16, 19, ? figs. 17, 18, *non* fig. 15.
1928 ? *Chonetoidea grayi* (Davidson) Jones : 500.
1928 *Chonetoidea* ? sp. 2 Jones : 502.
1963 *Chonetoidea grayi* (Davidson) ; Holland, Lawson & Walmsley : pl. 5, fig. 2.
1968 *Aegiria grayi* (Davidson) Cocks : pl. 12, fig. 3.

Diagnosis. *Aegiria* with relatively few ribs, which are angular at their crests and troughs. Bema poorly defined. Coarse brachial valve papillae are mainly subcircular rather than elongate.

Description. *Exterior.* Pedicle valve gently convex, brachial valve flat to slightly concave, both valves with slight median fold and sulcus. Outline semicircular, with only an hint of alation. Size is small for genus (maximum width less than 5 mm. in topotype collection of 35 specimens). Usually between 20 and 30 ribs, no specimen seen with more than 40, but counting is difficult near the alae, since the ribs are much finer there. Ribs more angular in cross section than *A. garthensis*. No rugae or undulations seen. Growth lines occasionally visible near anterior margin. Interarea relatively large, the two valves making shallow angles with each other. Small deltidium; no childidium or chilidial plates. Cardinal process clearly visible from valve exterior. Small but distinct apical foramen, probably functional, and protegular node at apex of brachial valve, forming base to cardinal process.

Pedicle Valve Interior. No evidence of hinge line denticulation. Teeth supported by dental plates which flare antero-laterally, merging slowly with valve floor as bounding ridges to posterolateral part of muscle field. Pedicle chamber bounded posteriorly by deltidium and laterally by teeth and dental plates. Some secondary calcite immediately anterior of pedicle opening, which falls away anteriorly before being raised again to form slight swell of the rather faint and short medium septum. Diductor scars lanceolate on either side of median septum between large adductor scars, at 60 to 90 degrees to each other. No vascular markings seen. Exterior ornament conspicuous from interior. Some papillae outside central muscle field, but much finer than in brachial valve.

Brachial Valve Interior. No fossettes seen on hinge line. Strong socket plates. Anterior to cardinal process a pit extends nearly to valve exterior at protegular node, anterior of which is strong median septum extending three quarters of the way to anterior margin. Small trace of side septa. Bema visible, but usually only faintly developed. Outside this several coarse papillae relatively amongst the largest of any strophomenide. These papillae subcircular, rather than elongate as *A. garthensis*. In Upper Llandovery (Plate 17, fig. 12) papillae pattern seems random, by Ludlow time, however, they are roughly arranged into two or more concentric rings (Plate 17, fig. 14). Faint radial striae sometimes seen on surface of bema, possibly reflection of exterior ornament or striations upon muscle field similar to *Leangella*. Vascular system not seen.

LECTOTYPE (here chosen) B 780, (Plate 17, fig. 9), a pair of conjoined valves from the Wenlock Limestone of Dudley, Worcestershire, England. John Gray collection, presented to the Museum in 1869. Davidson (1849 : 271) based his descriptions on specimens found by Gray and Fletcher at Dudley, and there is no material in the Davidson Collection.

LOCALITIES AND MATERIAL. Wenlock Limestone (Upper Wenlock), " Dudley ", Staffordshire, England. Gray and Caroline Birley Collections, no exact locality. (Plate 17, figs. 9, 10) (B 780, B 23205 etc.).

Hughley Shales (Llandovery, Telychian), stream bank at Domas, near Harley, Shropshire, England. Grid Ref. SJ/5936 0062. (Plate 17, fig. 8) (OUM C13403–56).

Hughley Shales (Llandovery, late Fronian or early Telychian), north bank of River Onny, Shropshire, England. Grid Ref. SO/4260 8532. (Plate 17, figs. 11, 12) (OUM C12046–C12155).

Hughley Shales (Llandovery, Telychian), south-west bank of Heath Brook, 500 yards ENE of the Plough Inn, Wall-under-Heywood, Shropshire, England. Grid Ref. SO/5120 9276. (OUM C13056–75).

C_3 Beds (Llandovery, Fronian) roadside outcrop on Cefn Cerig road, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/7751 3257. (BB 32116–35).

Chonetoidea grayi Beds (Ludlow, upper Leintwardinian), Pont Shoni, near Builth Wells, Radnorshire, Wales. Grid Ref. SO/078 468. (Plate 17, figs. 13–14). (BB 32430–1 etc.).

DIMENSIONS (in mm.)	l	w
B 780 conjoined valves lectotype (Plate 17, fig. 9), Dudley.	2·7	4·3
B 23205 conjoined valves (upper central specimen in Pl. 17, fig. 10) Dudley.	2·7	4·1
OUM C13974 conjoined valves (central specimen in Pl. 17, fig. 8) Hughley.	1·8	3·0
OUM C13425 (1st specimen) conjoined valves Domas.	1·9	2·9
OUM C13425 (2nd specimen) conjoined valves Domas.	1·4	2·3

DISCUSSION. The description is based on the topotype collection for the exterior, and on a collection from the Hughley Shales (Upper Llandovery) of the Onny River for the interior.

" *Chonetoidea* " *grayi* has been widely quoted in recent years from various horizons in the Silurian, chiefly from the British Ludlow ; indeed Chonetoidea grayi Beds is used as a rock formation name in the Builth district (Straw 1937).

The late Professor W. F. Whittard had already selected the lectotype, but he was kind enough to hand over his notes on the species to the present author. At the time of his original description, Davidson was not familiar with *Leptaena minima* J. de C. Sowerby 1839, but in his monograph (1871 : 335) he put *grayi* into the synonymy of *minima*, although not without doubts. An examination of the holotype of *minima* (GSM Geol. Soc. Coll. 6639) reveals different ribbing from *grayi* and also a spine base on the hinge line, indicating that *minima* is a chonetid, perhaps referable to *Protochonetes* Muir Wood 1962.

As may be seen from Plate 17, *Aegiria grayi* differs from the Lower Llandovery *A. garthensis* (and also *A. norvegica*) in its fewer and more angular ribs, and its less well defined bema. The form of *A. grayi* differs from the Upper Llandovery (Plate 17, figs. 11, 12) to the Ludlow (Plate 17, figs. 13, 14) and a study of the species group is intended by the present writer.

VII. ACKNOWLEDGMENTS

I am most grateful for valuable discussion with many people, in particular Dr. M. G. Bassett, Dr. M. J. S. Rudwick, Dr. J. T. Temple and Professor A. Williams. I also thank Dr. G. F. Elliott for a constructive reading of the manuscript. Dr. V. Havlíček and Dr. J. Bergström have kindly led me to localities in Bohemia and Gotland respectively.

I am obliged to the various authorities at museums ; Mr. J. M. Edmonds and Mr. H. P. Powell of the Oxford University Museum (OUM), Dr. A. W. A. Rushton, Mr. D. E. White, and Dr. P. T. Warren of the Geological Survey (GSM), Mr. A. G. Brighton and Dr. R. B. Rickards of the Sedgwick Museum, Cambridge (SM), Dr. J. K. Ingham of the Hunterian Museum Glasgow (HML), Dr. I. Strachan of the Geology Department, Birmingham University (BU), and Dr. V. Jaanusson of the Naturhistoriska Riksmuseet, Stockholm (RMS). Most of the material is in the British Museum (Natural History) (B and BB). In addition, Dr. A. Martinsson kindly searched in the Wahlenberg collection at Uppsala on my behalf, and Dr. G. A. Cooper sent some choice American specimens on exchange.

I have had valuable technical assistance from Miss L. M. Stokes. The photographs were taken by Messrs P. Green, C. Keates and T. Parmenter, as well as by myself ; Mr. Green also drew Text-figs. 1 and 2.

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PLATE 1

Merciella vesper Lamont and Gilbert

Llandovery, Telychian, Wych Beds, Coneygore Coppice, Worcestershire, England. Lamont & Gilbert Collection.

FIGS. 1, 2. BU 369. Latex cast and internal mould of brachial valve. Figured Lamont & Gilbert 1945 pl. 4, figs. 10, 12. Lectotype, × 4.0.

FIGS. 3, 4. BU 370. Latex cast and internal mould of brachial valve. Figured Lamont & Gilbert 1945 pl. 4, fig. 11. Fig. 3, × 4.0., Fig. 4, × 3.0.

FIG. 5. BU 367. Internal mould of pedicle valve. Figured Lamont & Gilbert 1945, pl. 4, fig. 8. × 4.0.

Leptellininid gen, et sp. indet.

Llandovery, Rhuddanian, Woodland Formation, Woodland Point, near Girvan, Ayrshire, Scotland. Grid Ref. NX/168 952. Mrs. R. Gray Collection.

FIGS. 6, 7. BB 31832. Latex cast and internal mould of brachial valve. Fig. 6 × 4.0, Fig. 7 × 2.1.

FIG. 8. BB 31831. Internal mould of pedicle valve. × 2.1.

Diambonia discuneata (Lamont)

Ashgill, Lower Drummuck Group, east brow of Quarrel Hill, near Girvan, Ayrshire, Scotland. Dr. A. Lamont Collection.

FIG. 9. HML 1983. Internal mould of pedicle valve. Figured Lamont 1935 pl. 7, figs. 18, 19. × 9.0.

FIG. 10. HML 1984. Internal mould of pedicle valve. × 9.0.

Leangella scissa (Davidson)

Llandovery, Rhuddanian, Gasworks Mudstone, opposite entrance to the gasworks, Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/9558 1533. Author's collection.

FIG. 11. BB 31824. Internal mould of pedicle valve. × 2.0.

FIG. 12. BB 31828. Internal mould of pedicle valve. × 3.0.

FIG. 13. BB 31827. Internal mould of brachial valve. × 3.0.

FIG. 14. BB 31829. Internal mould of brachial valve. × 3.0.

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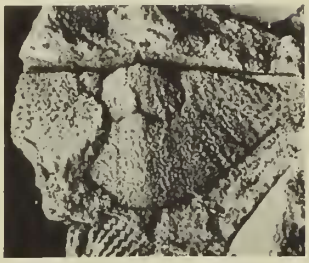

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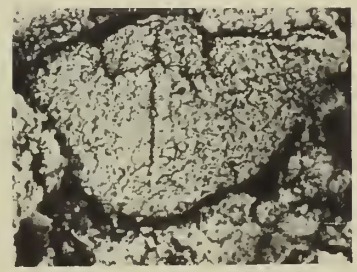

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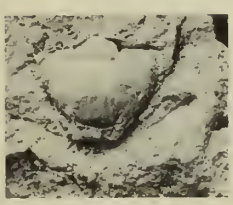

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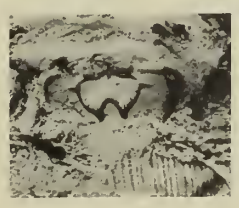

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PLATE 2

Leangella scissa (Davidson)

Llandovery, Rhuddanian, Gasworks Mudstone, opposite entrance to the gasworks, Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/9588 1533. Author's collection.

FIGS. 1, 4. BB 32167. Latex casts of the external and internal of a brachial valve. × 5.0.

FIG. 2. BB 31825. Internal mould of pedicle valve. × 3.0.

FIG. 3. BB 31826. Internal mould of brachial valve. × 3.0.

Llandovery, Rhuddanian, Woodland Formation, Woodland Point, Girvan, Ayrshire, Scotland. Grid. Ref. NX/168 952. Mrs. R. Gray collection.

FIG. 5. BB 44620. External view of pedicle valve, figured Reed 1917, pl. 14, fig. 36 (as *Plectambonites segmentum* var. *woodlandensis*, and selected as lectotype of that subspecies in this paper). × 3.0.

FIGS. 6, 7. BB 31836. Two views of an internal mould of a small specimen with conjoined valves. × 8.5.

Llandovery, late Idwian, Venusbank Formation, Hope Quarry, near Minsterley, Shropshire, England. Grid Ref. SJ/3551 0208. Author's collection, except for Fig. 13.

FIG. 8. OUM C9130. Internal mould of pedicle valve. × 4.0.

FIG. 9. OUM C9125. Internal mould of a large pedicle valve, with well impressed vascular system. × 3.0.

FIG. 10. OUM C9127. Internal mould of pedicle valve. × 4.0.

FIG. 11. OUM C9121. Internal mould of brachial valve. × 4.0.

FIG. 12. OUM C9123. Internal mould of pedicle valve. × 4.0.

FIG. 13. B 13673. Internal mould of pedicle valve figured Davidson 1883, pl. 12, fig. 22 (as *Leptaena scissa* Salter). × 6.0.

FIG. 14. OUM C9136. Internal mould of pedicle valve. × 4.0.

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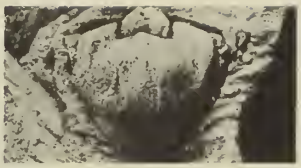

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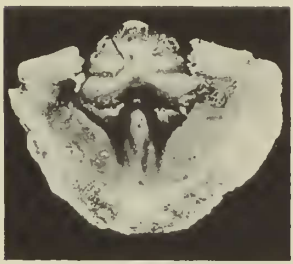

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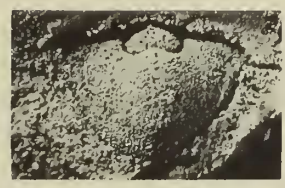

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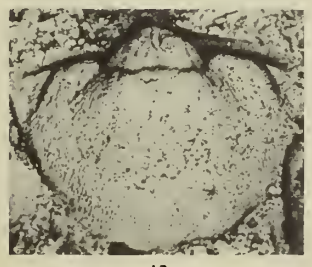

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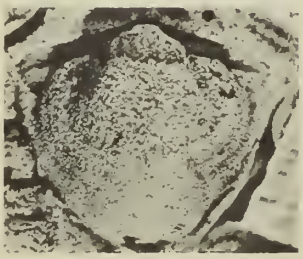

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PLATE 3

Leangella segmentum (Lindström)

Wenlock Limestone (exact locality unknown), Dudley, Staffordshire, England. John Gray Collection.

FIG. 1. B 770. Internal view of a brachial valve. × 5.7.

Leangella scissa (Davidson)

Llandovery, Late Rhuddanian or early Idwian, Newlands Sandstone, near Newlands Farm, Craighead Inlier, near Girvan, Ayrshire, Scotland. Grid Ref. NS/2777 0432. Mrs. R. Gray Collection.

FIGS. 2, 3. B 73644. Internal mould of pedicle valve, from above and behind. × 6.6.

FIG. 4. B 73641. Internal mould of brachial valve. × 5.0.

Llandovery, early Fronian, Venusbank Formation, temporary exposure in field, near Wilmington, Shropshire, England. Grid Ref. SJ/3061 0246. W. F. Whittard Collection.

FIGS. 5, 6. GSM 85286. Latex cast and internal mould of brachial valve. × 2.8.

FIGS. 7–9. GSM 85287. Internal mould and two views of latex cast of a brachial valve. Figs. 7 and 8 × 3.3, Fig. 9 × 7.0.

FIG. 10. GSM 85288. Internal mould of conjoined valves. × 5.1.

Llandovery, early Telychian, C_4 Beds, abandoned quarry on west side of Cefn-Cerig road, near Llandovery, Carmarthenshire, Wales, Grid Ref. SN/7741 3235. Author's collection.

FIG. 11. BB 31675–6. Internal mould of brachial valve. Beneath it is an internal mould of a brachial valve of *Eoplectodonta penkillensis*. × 4.1.

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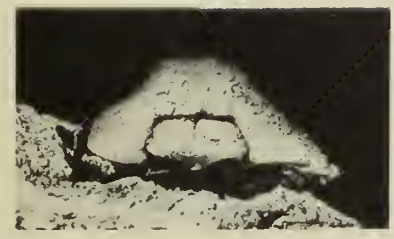

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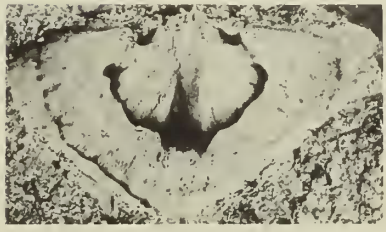

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PLATE 4

Leangella scissa (Davidson)

Llandovery (Fronian). C. Beds, near old footbridge south of Lletty'r-hyddod, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/7418 2812. Author's collection.

FIGS. 1, 2. BB 32095. Two views of an internal mould of a pedicle valve. × 6.0.

FIG. 3. BB 32097. Brachial internal mould, × 9.0.

FIG. 4. BB 32103. Pedicle internal mould, × 5.8.

Leangella tufolepta (Havlíček)

Wenlock, Upper Liteň Formation, locality " Hlinik ", near Svaty Jan pod. Skalou, Czechoslovakia. Author's collection.

FIG. 5. BB 32216. Pedicle internal mould, × 5.5.

FIG. 6. BB 32215. Internal mould of conjoined valves, broken off at the subperipheral rim (mounted on a piece of plasticene). × 6.7.

Leangella segmentum (Lindström)

Wenlock, Mulde Marl, Djupvik, Isle of Gotland, Sweden. Angelin Collection, used by Lindström.

FIGS. 7, 8. RMS Br31602. External views of conjoined valves, × 4.5.

FIG. 9. RMS Br31599. Internal view of brachial valve, × 5.0.

FIG. 10. RMS Br31600. Internal view of brachial valve, × 4.9.

FIG. 11. RMS Br31598. Internal view of brachial valve, lectotype. × 4.6.

FIG. 12. RMS Br31601. Internal view of brachial valve, × 5.7.

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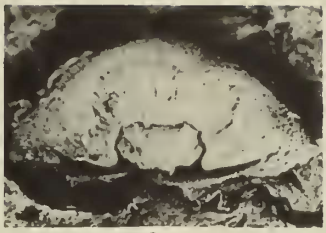

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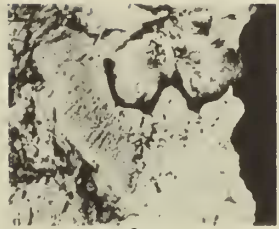

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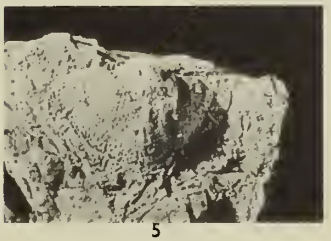

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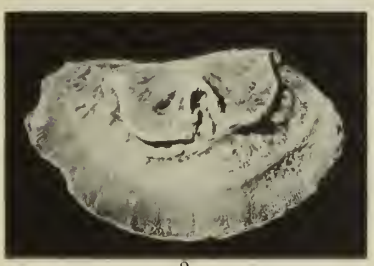

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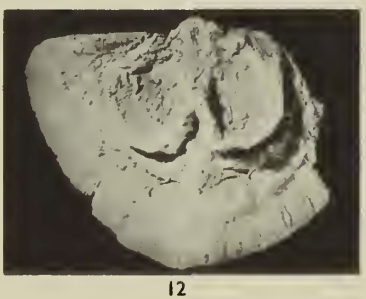

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PLATE 5

Eoplectodonta duplicata (J. de C. Sowerby)

Llandovery, Rhuddanian, " Cefn Rhyddan ", Llandovery, Carmarthenshire, Wales. Sir R. I. Murchison Collection.

Fig. 1. GSM Geol. Soc. Coll. 6877. External mould of brachial valve. Figured J. de C. Sowerby (*in* Murchison) 1839, pl. 19, fig. 2 (as *Leptaena sericea* var.) × 3.2.

Fig. 2. GSM Geol. Soc. Coll. 6874. Internal mould of pedicle valve. Figured J. de C. Sowerby (*in* Murchison) 1839, pl. 22, fig. 2. Holotype. × 3.4.

Llandovery, Rhuddanian, Gasworks Mudstone, opposite entrance to the gasworks, Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/9588 1533. Author's collection.

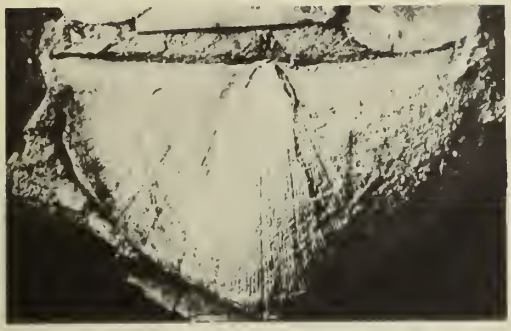
Figs. 3, 6. BB 31701. Internal mould and latex cast of brachial valve, × 2.0.

Figs. 4, 7. BB 31699. Internal mould and latex cast of brachial valve. × 2.0.

Figs. 5, 8. BB 31695. Internal mould and latex cast of brachial valve. × 2.0.

Figs. 9, 10. BB 31700. Internal mould and latex cast of brachial valve. × 4.0.

Figs. 11, 12. BB 31696. Internal mould and latex cast of brachial valve. × 4.0.



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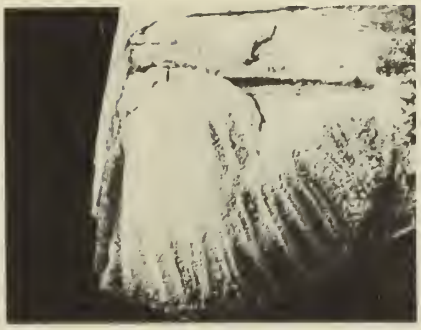

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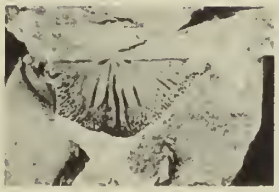

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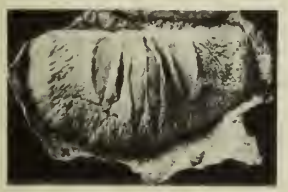

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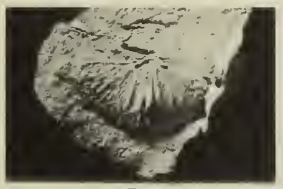

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PLATE 6

Eoplectodonta duplicata (J. de C. Sowerby)

Llandovery, Rhuddanian, Gasworks Mudstone, opposite entrance to the gasworks, Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/9588 1533. Collected by C. P. Nuttall and the author.

FIG. 1. BB 31673. Internal mould of pedicle valve with well impressed vascular system. × 3.0.

FIG. 2. BB 31674. Internal mould of pedicle valve. × 3.0.

FIG. 3. BB 31732. Internal mould of pedicle valves. × 1.6.

FIGS. 4–6. BB 31670. Internal mould of brachial valve, and latex cast of it. Fig. 6 is a view of the latex cast from the side, showing the posterior geniculation of the septal field, and its anterior curve, which closely parallelled that of the pedicle valve. Fig. 4 × 3.1., Fig. 5 × 4.2 and Fig. 6 × 2.6.

FIG. 7. BB 31740. Internal mould of pedicle valve. × 1.6.

FIG. 8. BB 31753. Internal mould of pedicle valve. × 1.6.

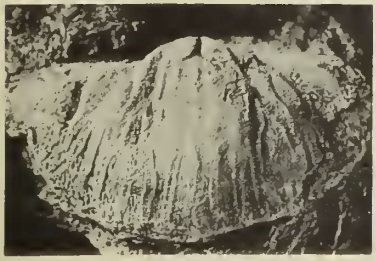
Llandovery, Rhuddanian, Gasworks Mudstone, north end of railway cutting, 150 yards southwest of Haverfordwest Station, Pembrokeshire, Wales. Grid Ref. SM/9588 1563.

FIGS. 9, 14. GSM 37567. Internal mould of pedicle valve, and external mould of brachial valve. The pedicle valve is the holotype of *Sowerbyella precursor* Jones 1928, plate 23, fig. 3 × 2.3. T. C. Cantrill collection.

FIGS. 10, 11. BB 32055. External mould and latex cast of brachial valve, with associated pedicle interarea. × 2.6. Author's collection.

FIG. 12. GSM TCC 1205. Internal mould of brachial valve, × 5.3. T. C. Cantrill collection.

FIG. 13. GSM TCC 1198. Internal mould of pedicle valve, × 3.5. T. C. Cantrill collection.



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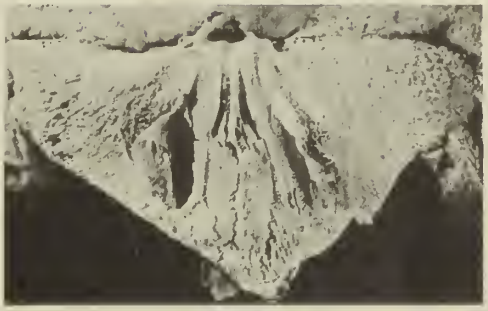

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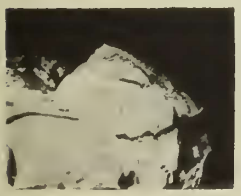

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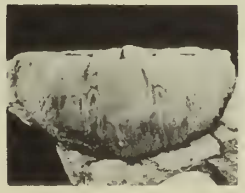

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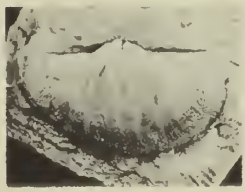

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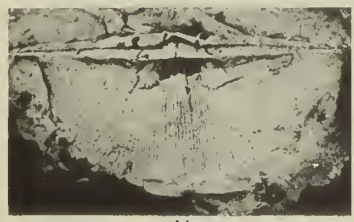

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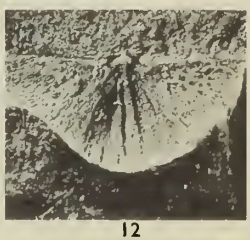

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PLATE 7

Eoplectodonta duplicata (J. de C. Sowerby)

Llandovery, Rhuddanian, Woodland Formation, Woodland Point, Girvan, Ayrshire, Scotland. Grid Ref. NX/168 952. Mrs. R. Gray collection.

FIG. 1. B 44729. External view of pedicle valve. × 2.8.

FIG. 2. B 44734. External view of pedicle valve, × 2.8.

FIG. 3. BB 31830. Internal mould of pedicle valve, with polyzoan colony, × 2.0.

FIGS. 4, 5. BB 31833. Two views of the internal mould of small conjoined valves, × 3.0.

FIGS. 6, 8. BB 31834. Two views of the internal mould of conjoined valves, × 3.0.

FIGS. 7, 9. BB 31835. Two views of the internal mould of conjoined valves, × 3.0.

FIGS. 10, 11. BB 31985. Latex cast and external mould of brachial valve, × 2.5.

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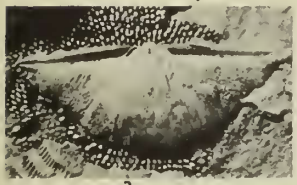

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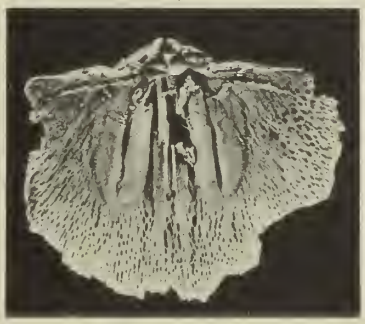

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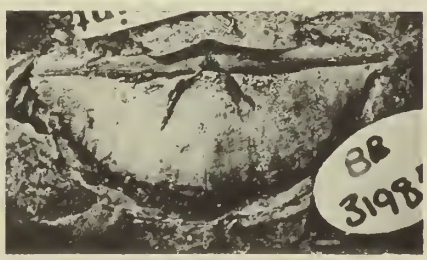

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PLATE 8

Eoplectodonta duplicata (J. de C. Sowerby)

Llandovery, Rhuddanian, Woodland Formation, Woodland Point, Girvan, Ayrshire, Scotland. Grid Ref. NX/168 952. Mrs. R. Gray collection.

FIG. 1. B 73537. External view of pedicle valve, figured Reed 1917, pl. 16, fig. 9 as *Plectambonites transversalis* var. *tricostata*. × 3.7.

FIG. 2. B 73539. External view of pedicle valve, figured Reed 1917, pl. 16, fig. 8 as *Plectambonites transversalis* var. *tricostata*, and selected as lectotype of the subspecies in this paper. × 3.4.

FIGS. 3, 4. BB 31990. Pedicle internal mould and latex cast, × 2.2 and 2.7.

Llandovery, Rhuddanian, Gasworks Sandstone, Union Hill, Haverfordwest, Pembrokeshire, Wales. J. Pringle Collection.

FIGS. 5, 6. GSM 37580. Latex cast and internal mould of brachial valve, figured Jones 1928, pl. 23, fig. 11 as *Sowerbyella superstes*. × 4.8 and 2.5.

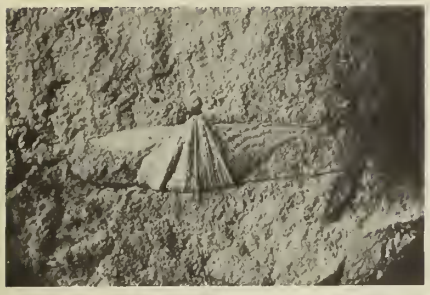
FIGS. 7, 8. GSM 37579. Two pedicle internal moulds on the same slab, fig. 7 is the holotype of *Sowerbyella superstes* Jones, figured Jones 1928, pl. 23, figs. 10, 10a. × 2.9.

Llandovery, Rhuddanian, Mulloch Hill Group, Mulloch Hill, nr. Girvan, Ayrshire, Scotland. Grid Ref. NS/2703 0399. Mrs. R. Gray Collection.

FIG. 9. B 44648. External mould of brachial valve, the counterpart to the specimen figured by Reed 1917, pl. 15, fig. 42 as *Plectambonites transversalis* var. *mullochensis*. × 3.0.

FIG. 10. B 44649. Exterior of pedicle valve, figured Reed 1917, pl. 16, fig. 2 as *Plectambonites transversalis* var. *mullochensis* × 2.1.

FIG. 11. B 44718. Pedicle internal mould, figured Reed 1917, pl. 15, fig. 41 as *Plectambonites transversalis* var. *mullochensis*, and selected as lectotype of that subspecies in this paper. × 2.5.



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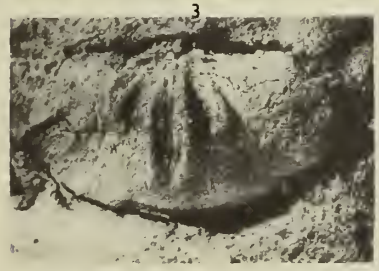

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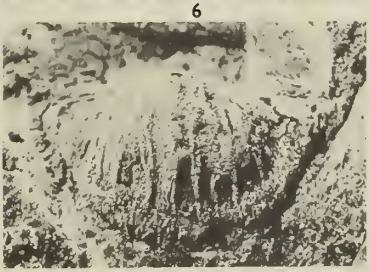

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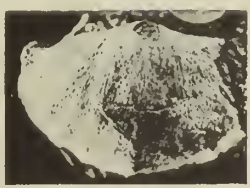

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PLATE 9

Eoplectodonta penkillensis (Reed)

Llandovery, Telychian, Uzmaston Beds, 100 yards NW of Haroldston St. Issels Church, near Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/9636 1409. O. T. Jones Collection.

FIG. 1. GSM 37557. Pedicle internal mould, figured Jones 1928 pl. 23, fig. 15 as *Sowerbyella millinensis*. × 4.1.

FIGS. 2, 5. GSM 37559. Latex cast and internal mould of brachial valve, figured Jones 1928, pl. 23, fig. 16 as *Sowerbyella millinensis*. × 5.7 and 4.2.

FIG. 4. GSM 37556. Brachial external mould. × 4.4.

Llandovery, Telychian, Canaston Beds, road cutting opposite Canaston Farm, near Narberth, Pembrokeshire, Wales. Grid Ref. SN/0697 1483.

FIG. 3. GSM 37531. External mould of brachial valve, figured Jones 1928, pl. 23, fig. 22 as the holotype of *Sowerbyella millinensis* var. *canastonensis*. O. T. Jones Collection. × 2.6.

FIG. 6. GSM 37531 (another specimen on the same slab as the last). Internal mould of pedicle valve, figured Jones 1928, pl. 23, fig. 21 as *Sowerbyella millinensis* var. *canastonensis*. O. T. Jones Collection. × 5.1.

FIGS. 7, 10. BB 32418. Latex cast and internal mould of brachial valve. Author's Collection. × 2.6 and 2.8.

Llandovery, Telychian, Uzmaston Beds, near ruins of mill, 200 yds W. by N. of Millin Farm, 3 miles ESE of Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/9943 1418.

FIG. 9. GSM 37540. External mould of brachial valve, figured Jones 1928, pl. 23, fig. 18 as the holotype of *Sowerbyella millinensis* var. *parabola*. O. T. Jones Collection. × 3.0.

FIGS. 8, 11. BB 32419. Internal mould of brachial valve. Author's Collection. × 4.0 and 4.4.

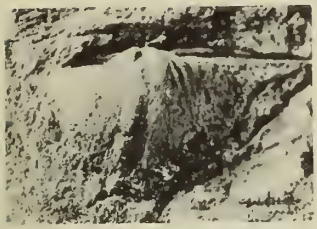
FIG. 12. GSM 37541. Internal mould of pedicle valve, figured Jones 1928, pl. 23, fig. 20 as *Sowerbyella millinensis* var. *parabola*. O. T. Jones Collection. × 1.6.

Llandovery, Telychian, Canaston Beds, South bank of the Eastern Cleddau, Pembrokeshire, Wales. Grid Ref. SN/0485 1385. Author's Collection.

FIG. 13. BB 32226. External mould of brachial valve. × 3.7.

FIG. 14. BB 31839. Internal mould of brachial valve, with conjoined pedicle valve. × 2.0.

FIG. 15. BB 32227. External mould of brachial valve, with conjoined pedicle valve, showing the interarea. × 3.8.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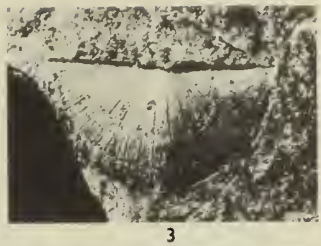
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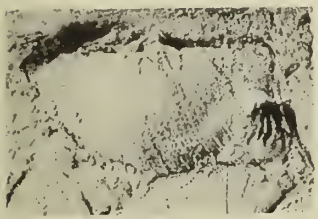
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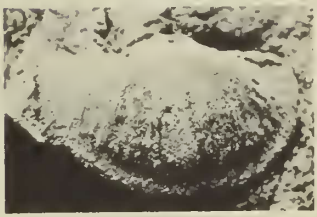
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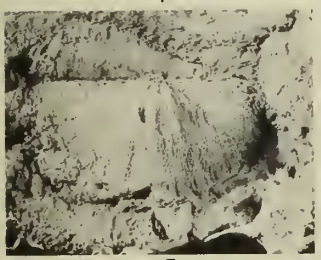
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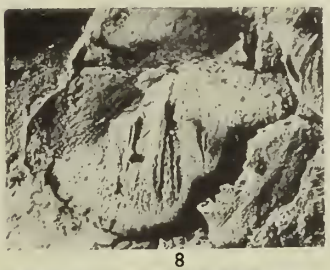
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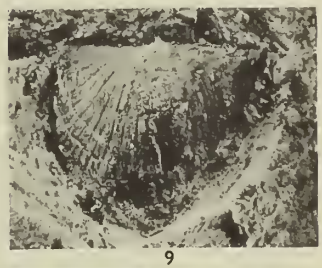
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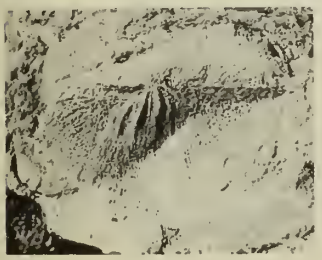
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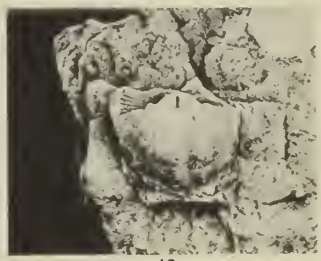
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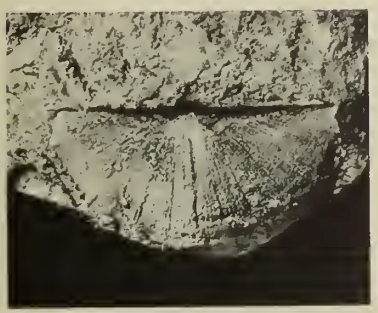
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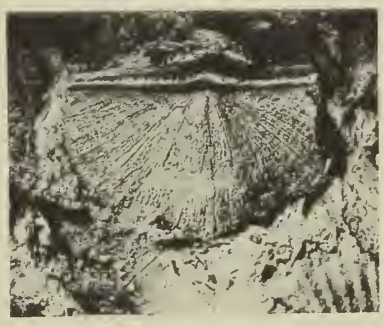
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PLATE 10

Eoplectodonta penkillensis (Reed)

Llandovery, Telychian, Canaston Beds, south bank of the Eastern Cleddau, Pembrokeshire, Wales. Grid Ref. SN/0485 1385. Author's Collection.

FIG. 1. BB 32228. Internal mould of pedicle valve. × 3.5.
FIG. 2. BB 32219. Internal mould of pedicle valve. × 4.2.
FIG. 3. BB 32221. Internal mould of pedicle valve. × 4.0.

Llandovery, Fronian, Pentamerus Beds, Hurst Coppice, Shropshire, England. Grid Ref. SJ/6271 0585. W. F. Whittard Collection.

FIG. 4. BB 32231. Internal mould of brachial valve. × 4.8.

Llandovery, Fronian, Pentamerus Beds, stream exposure in Harper's Dingle, Shropshire, England. Grid Ref. SJ/6314 0669. W. F. Whittard Collection.

FIG. 5. BB 31841. Exterior of pedicle valve. × 2.0.

Llandovery, Lower Telychian, Pentamerus Beds, stream exposure in Sheinton Brook, SE of Cressage, Shropshire. Grid Ref. SJ/6116 0310. Author's Collection.

FIG. 6. OUM C14337. Internal mould of pedicle valve. × 4.0.
FIG. 10. OUM C14396. Internal mould of brachial valve. × 4.0.

Llandovery, Lower Telychian, Hughley Shale, river bank above the unconformity with the Ordovician, Onny River, Shropshire, England. Grid Ref. SO/4260 8532. Author's Collection.

FIGS. 7, 8. OUM C11970. External and internal moulds of a brachial valve. × 4.0.
FIG. 9. OUM C11965. Internal mould of brachial valve. × 3.0.
FIGS. 11, 12. OUM C11962. External and internal moulds of a brachial valve. × 5.0.

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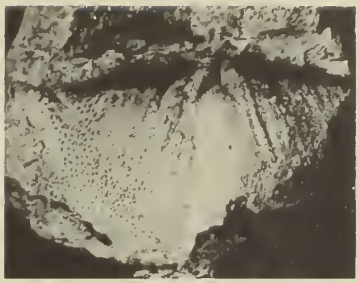

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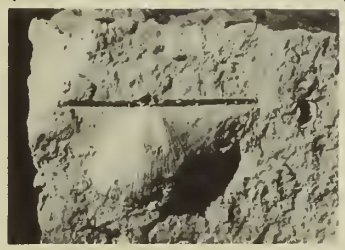

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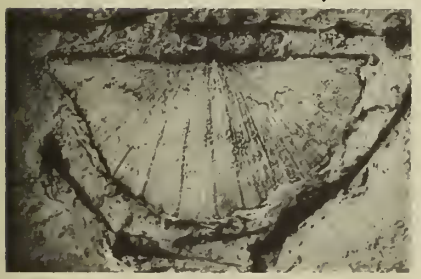

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PLATE 11

Eoplectodonta penkillensis (Reed)

Llandovery, Telychian, stream exposure near Domas, Shropshire, England. Grid Ref. SJ/5936 0062. Author's Collection.

Fig. 1. OUM C13614–5. Slab with three pedicle internal moulds and two brachial external moulds. At the top is a fragment of *Amphistrophia whittardi* Cocks. × 1.3.

Fig. 2. BB 32222. Internal mould of brachial valve. × 4.8.

Llandovery, Telychian, Hughley Shale, stream exposure near Hughley, Shropshire, England. Grid Ref. SO/5605 9747. Author's Collection.

Fig. 3. OUM C13700. Internal mould of pedicle valve. × 4.4.

Fig. 4. BB 31840. Exterior of pedicle valve. × 2.2.

Fig. 7. BB 31838. Exterior of pedicle valve. × 2.2.

Llandovery, Telychian, Wych Beds, bank on south side of football pitch at Cowleigh Park, Malvern Hills, Herefordshire, England. Grid Ref. SO/7616 4723. A. M. Ziegler Collection.

Figs. 5, 8. OUM C4896. Internal mould and latex cast of pedicle valve. × 2.1.

Figs. 6, 9. OUM C4857. Internal mould and latex cast of brachial valve. × 3.7.

Fig. 10. OUM C4859. External view of part of a brachial valve, showing the ornament. Many of the moulds of exteriors at this locality do not show any ornament, this is due to the mode of preservation only, as can be seen from this specimen. × 2.5.

Fig. 11. OUM C4872. Internal mould of brachial valve. × 1.9.

Fig. 12. OUM C4890. Internal mould of pedicle valve. × 2.0.

Fig. 13. OUM C4863. Internal mould of brachial valve. × 2.0.

Llandovery, Fronian, " Camregan Group ", Bargany Pond Burn, near Girvan, Ayrshire, Scotland. Grid Ref. NX/2500 9858. Mrs. R. Gray Collection.

Fig. 14. B 44710. Partly exfoliated exterior of pedicle valve, figured Reed 1917, pl. 16, fig. 3, as *Plectambonites transversalis* var. *penkillensis*. Selected lectotype in this paper. × 2.0.

Fig. 15. B 44711. External mould of brachial valve, figured Reed 1917, pl. 16, fig. 4. × 3.5.

Fig. 16. B 44712. Internal mould of pedicle valve, figured Reed 1917, pl. 16, fig. 5. × 2.3.

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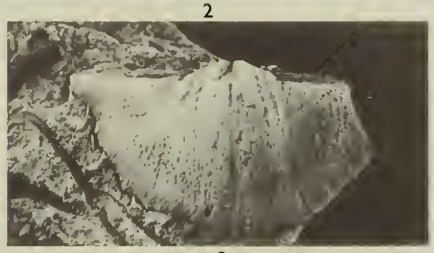

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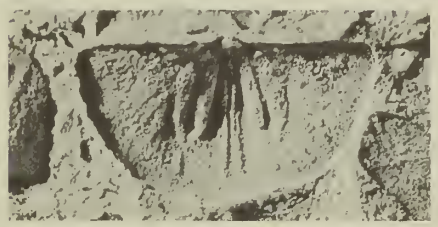

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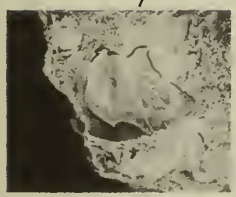

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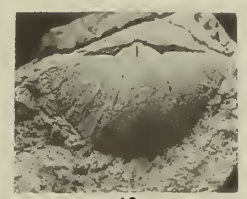

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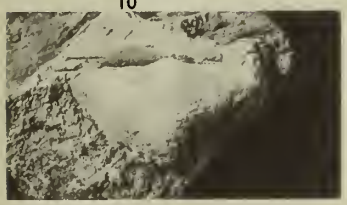

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PLATE 12

Eoplectodonta transversalis (Wahlenberg)

Llandovery, Telychian, Lower Visby Marl, the specimens labelled " Lundbjars " from beach exposure, 1 km west of Lundbjars, Gotland, Sweden. Grid Ref. CK/465 062. The specimens labelled " Nyhamn " are from beach exposure north of Nyhamn, Gotland, Sweden. Grid Ref. CK/663 055. Author's collection.

FIGS. 1–3. RMS Br 102394. Three views of conjoined valves, neotype. × 3.0. Lundbjars.

FIGS. 4, 5. BB 32420. Views of a brachial valve from above and behind. × 3.0 and 2.0. Lundbjars.

FIG. 6. BB 32425. Interior view of brachial valve, showing encrusting rim of polyzoa round the anterior margin. × 3.0. Nyhamn.

FIG. 7. BB 32426. Interior view of brachial valve. × 3.0. Nyhamn.

FIG. 8. BB 32421. Interior view of brachial valve. × 3.0. Lundbjars.

FIG. 9. BB 32427. View of conjoined valves. × 3.0. Nyhamn.

FIG. 10. BB 32428. Interior view of pedicle valve. × 2.5. Nyhamn.

FIG. 11. BB 32422. View of conjoined valves. × 3.0. Lundbjars.

FIG. 12. BB 32423. Interior view of pedicle valve. × 3.0. Lundbjars.

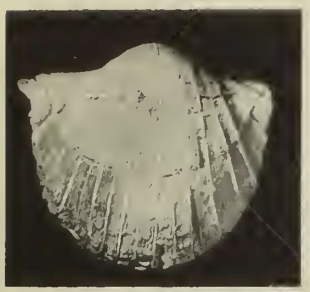
FIG. 13. BB 32424. Interior view of pedicle valve. × 5.0. Lundbjars.

Eoplectodonta duvalii (Davidson)

Wenlock, Slite Marl, ditch in coppice 1.6 km south of Västergarn, Gotland, Sweden. Grid Ref. CJ/292 688. Author's collection.

FIGS. 14, 15. BB 31837. Views of a brachial valve from above and behind. × 3.0.

FIG. 16. BB 32429. View of conjoined valves. × 3.0.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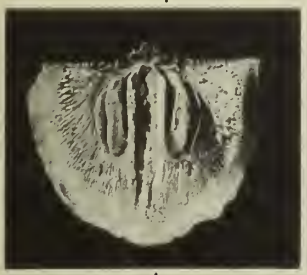
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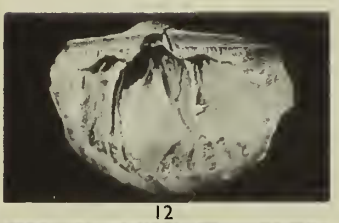
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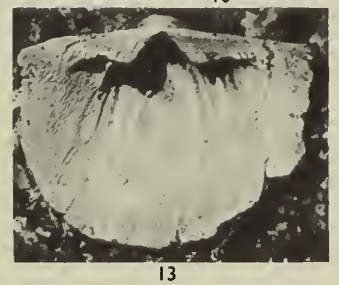
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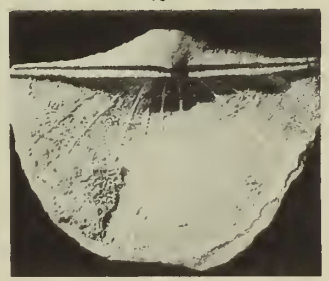
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PLATE 13

Eoplectodonta aff. ***duvalii*** (Davidson)

Wenlock, Upper Visby Marl, no precise locality except Gotland, Sweden. Old collection curated by Lindström.

FIG. 1 RMS Br 31048. Interal view of brachial valve. × 2.8.

Eoplectodonta sowerbyana (Barrande)

Wenlock, Upper Liteň Formation, locality " Hlink ", near Svaty Jan pod Skalou, Bohemia, Czechoslovakia. Author's collection.

FIGS. 2, 4. BB 32415. Pedicle internal mould, viewed from above and behind. × 4.0.

FIG. 5. BB 32413. Internal mould of brachial valve. × 3.3.

FIG. 6. BB 32414. Internal mould of pedicle valve. × 1.7.

FIG. 8. BB 32412. Internal mould of brachial valve. × 3.00, with the median septum clearly visible.

FIG. 9. BB 32411. Latex cast of brachial internal mould. × 1.9.

Eoplectodonta aff. ***duvalii*** (Davidson)

Wenlock, Kitaigorod Formation, Restevo Beds, left bank of the Ternava River, Kitaigorod Village, Podolia, U.S.S.R. Collected by Dr. P. T. Warren, 1968.

FIG. 3. GSM FOR L 64. External view of pedicle valve. × 3.3.

Eoplectodonta duvalii (Davidson)

Lower Wenlock, Buildwas Beds, north bank of River Severn, Shropshire, England. J. Gray Collection.

FIG. 7. GSM 12697. External view of pedicle valve of a pair of conjoined valves. Figured Jones 1928, pl. 24, fig. 2 as the holotype of *Sowerbyella transversalis* var. *lata*. × 2.0.

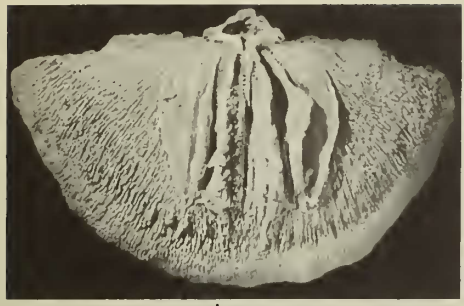
Wenlock Shale, Walsall, Staffordshire, England. T. Davidson Collection.

FIG. 10. B 13730. Pedicle valve embedded in matrix. Holotype, figured Davidson 1847, pl. 12, figs. 20, 21 and refigured Davidson 1848 and 1871. × 2.4.

? Ygerodiscus cornutus (Davidson)

Middle Wenlock, Wenlock Shale, " half a mile west of Buildwas Abbey ", Shropshire, England. T. Davidson Collection (from the washings by G. Maw).

FIGS. 11, 12. BB 32416. Views of conjoined valves from above and below, lectotype. × 4.6.



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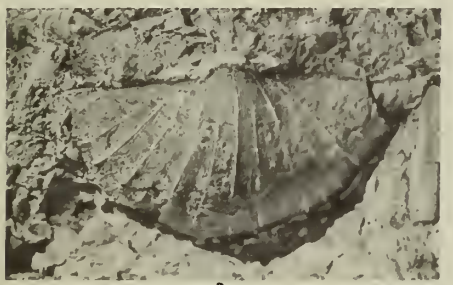

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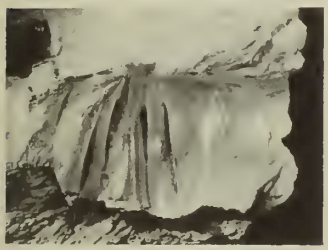

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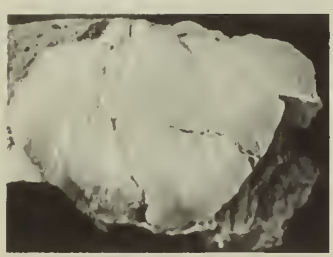

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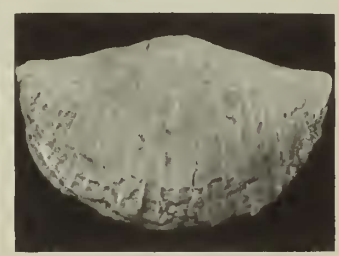

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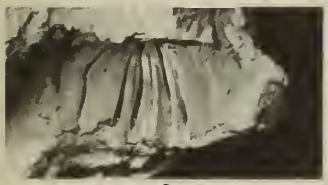

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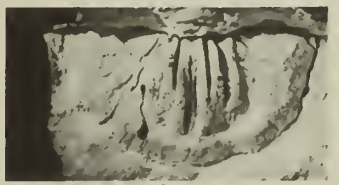

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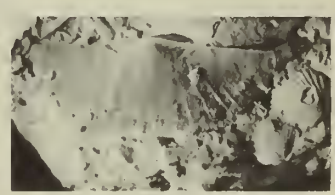

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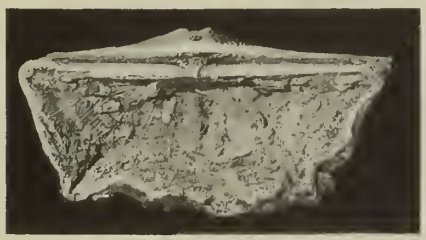

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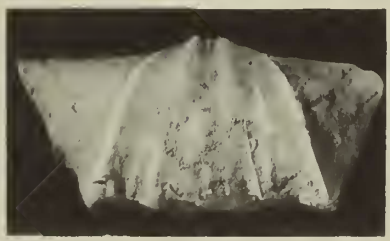

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PLATE 14

? Ygerodiscus cornutus (Davidson)

Middle Wenlock, Coalbrookdale Beds, " half a mile west of Buildwas Abbey ", Shropshire, England. Davidson Collection (from the washings by G. Maw).

Figs. 1, 2. B 5828. Views of conjoined valves from above and below. × 6.5.

Ygerodiscus undulatus (Salter)

Llandovery (late Idwian or early Fronian), Rosemarket Beds, old quarry, 700 yards south of Bullford, near Haverfordwest, Pembrokeshire, Wales. Grid ref. SM/9218 0980. O. T. Jones Collection.

Figs. 3, 4, 6, 7. GSM 37560–1. Latex casts and natural moulds of the exterior and interior of a brachial valve, the holotype of *Sowerbyella compressa*, figured Jones 1928, pl. 24, figs. 12 and 13. Despite being registered separately and only the exterior being designated as the holotype, the two specimens are part and counterpart. × 5.0, 3.5, 6.0 and 5.0.

Figs. 5, 8. GSM 37562–3. External and internal moulds of a brachial valve, figure 5 also shows part of the exterior of the pedicle valve, which is gaping wide open from the brachial valve. Figured Jones 1928, pl. 24, figs. 10, 11, and selected here as lectotype of *Sowerbyella plicata* Jones. Despite the separate registrations, the two specimens are part and counterpart. × 3.1 and 4.4.

Figs. 9, 11. GSM OTJ1030. Internal mould of brachial valve and latex cast of it. × 5.0.

Landovery, Fronian, C_1 beds, " near footbridge " (now disappeared) River Sefin, south of Lletty'rhyddod, Llandovery, Carmarthenshire, Wales. Grid Ref. SN/7418 2817. Author's collection.

Figs. 10, 12. BB 32417. Latex cast of internal mould and external mould of a brachial valve. × 5.5 and 6.0.

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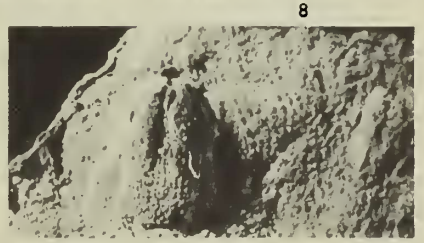

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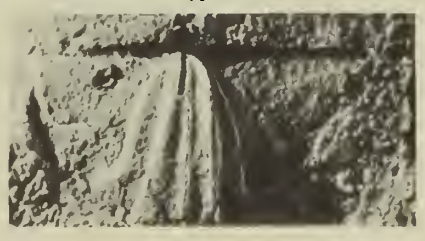

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PLATE 15

Ygerodiscus undulatus (Salter)

Llandovery, probably Idwian, but may be late Rhuddanian, " Mathyrafal ", Meifod, Montgomeryshire, Wales. M'Coy Collection.

FIG. 2. SMA 11308. External mould of a brachial valve, figured M'Coy 1852, pl. iH, figs. 31, 31a as *Leptaena quinquecostata*, figured Jones 1928 pl. 24, fig. 7 as the holotype of *Sowerbyella undulata* var. *maccoyi*. × 3.5.

FIG. 5. SMA 11307. External mould of a brachial valve, figured M'Coy 1852, pl. iH, fig. 30 as *Leptaena quinquecostata*, selected as lectotype by Jones 1928 : 455 and figured by him pl. 24, fig. 3. × 2.5.

Llandovery, probably Idwian, but may be late Rhuddanian, east bank of River Banwy, west of Upper Hill Farm, near Meiford, Montgomeryshire, Wales. This is probably the same locality as the one above from which M'Coy collected his specimens labelled " Mathyrafal ". Grid Ref. SJ/1327 1057. Author's collection.

FIG. 1. BB 31669. Internal mould of pedicle valve. × 4.6.

FIG. 4. BB 31919. Internal mould of brachial valve. × 4.0.

FIGS. 7–9. BB 31906. Two views of a pedicle internal mould and a latex cast of it. Figs. 7 and 8 × 6.3, fig. 9 × 5.0.

Llandovery, Idwian, B Beds, exposure on forestry track, northern area, near Llandovery, Carmarthenshire, Wales. Grid Ref. SN/8344 3726. Author's collection.

FIG. 3. BB 32109. Internal mould of pedicle valve. × 4.2.

Llandovery, late Idwian or early Fronian, Rosemarket Beds, old quarry, 700 yards south of Bullford, near Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/9218 0980.

FIG. 6. GSM OTJ1018. External mould of brachial valve. × 3.0. O. T. Jones Collection.

FIGS. 10–12. BB 32084. Latex cast of external mould and latex cast and internal mould of pedicle valve. Figs. 10, 11 × 4.6, fig. 12 × 5.6. Author's collection.

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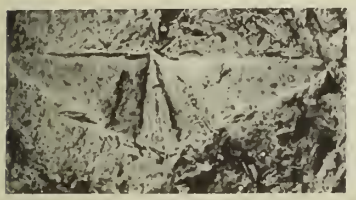

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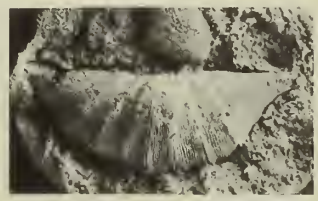

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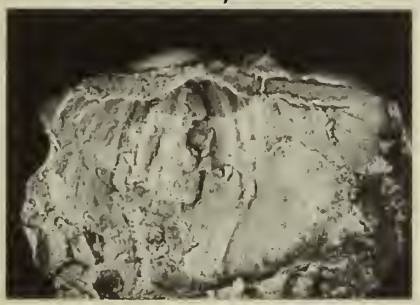

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PLATE 16

Anisopleurella gracilis (Jones)

Llandovery, Rhuddanian, Cartlett Mudstones, south side of railway cutting, 1 mile south of Haverfordwest, Pembrokeshire, Wales. Grid Ref. SM/956 146.

FIG. 1. GSM 37554. Specimen showing external mould of the brachial valve in the centre, on which is seen the impression of the outer side septa after presumably post-mortem crushing, with, as an outside rim, part of the internal mould of the pedicle valve. Counterpart to the holotype. O. T. Jones Collection. × 3.4.

FIG. 2. GSM 37552. Internal mould of pedicle valve, showing denticles. Figured Jones 1928, pl. 24, fig. 25. O. T. Jones Collection. × 6.2.

FIG. 3. GSM 37553. External mould of brachial valve, showing impression of outer side septa after crushing and also the conjoined interarea of the pedicle valve. Figured Jones 1928, pl. 24, fig. 24 as a pedicle valve. O. T. Jones Collection. × 4.9.

FIGS. 4, 7. GSM 37551. External mould of pedicle valve and latex cast of it, showing the median septum, inner side septa and outer side septa impressed after crushing. Figured Jones 1928, pl. 24, fig. 23. × 4.5 and 3.5.

FIG. 5. GSM OTJ766. External mould of brachial valve with associated pedicle valve interarea. O. T. Jones Collection. × 3.0.

FIGS. 6, 9. GSM 37555. Brachial valve internal mould and latex cast of it, the internal mould figured Jones 1928, pl. 24, fig. 22. O. T. Jones Collection. × 5.0 and 4.0.

FIG. 8. BB 32052. Latex cast of external mould of pedicle valve, showing impression of brachial valve median septum and both sets of side septa. Author's Collection. × 5.0.

Plectodonta mariae Kozlowski

Lower Devonian, Borszczow Stage, river bank, Krzywce, Podolia, U.S.S.R. (formerly Poland). Kozlowski Collection, in exchange with University of Warsaw 1932.

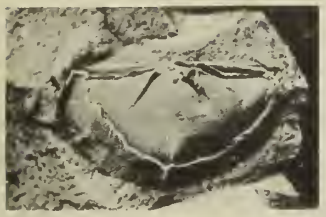
FIGS. 10, 11. B 81371. Two views of a pair of conjoined valves. × 4.4.

FIG. 12. B 81372. Interior of brachial valve. × 8.7.

? Aegiromena sp.

Llandovery, Idwian, Newlands Sandstone, near Newlands Farm, Craighead Inlier, near Girvan Ayrshire, Scotland. Grid Ref. NS/2777 0432. E. O. Lundholme Collection.

FIGS. 13, 14. HML 9931. External and internal moulds of a pedicle valve. × 5.8.



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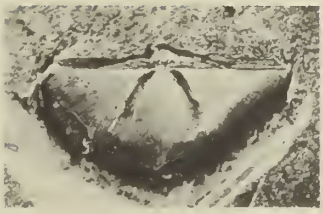

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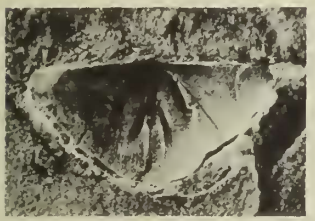

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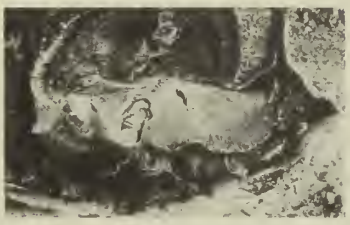

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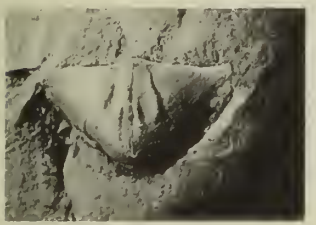

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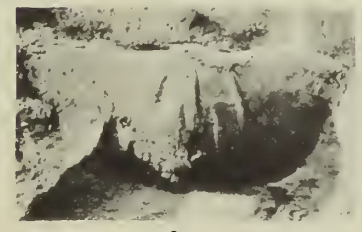

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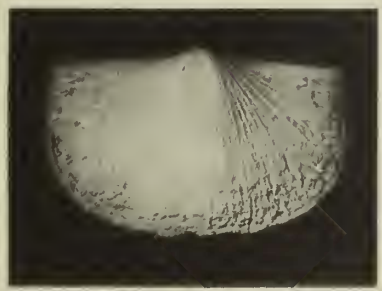

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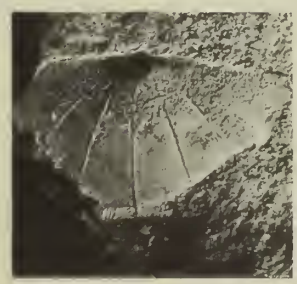

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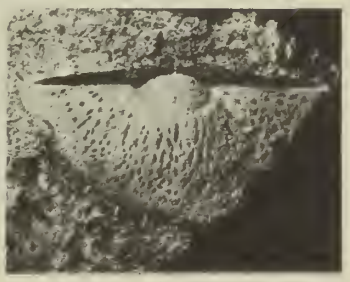

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PLATE 17

Chonetoidea papillosa (Reed)

Ashgill, Slade Beds, quarry at Upper Slade, near Haverfordwest, Pembrokeshire, Wales. Turnbull Collection.

FIG. 1. SMA 11311. Interior of brachial valve, lectotype, figured Reed 1905, pl. 23, fig. 13 and Jones 1928, pl. 25, fig. 21. × 10.

FIG. 2. SMA 11313. Interiors of both brachial and pedicle valves, syntype, figured Reed 1905, pl. 23, fig. 15 and Jones 1928, pl. 25, fig. 24. × 4.0.

FIG. 3. SMA 30841. Exterior mould of pedicle valve. × 4.2.

Aegiria garthensis (Jones)

Llandovery, Rhuddanian, " north of Garth ", Breconshire, Wales. G. Andrew Collection.

FIGS. 4 and 7. GSM 50417 and 50418. Exterior and interior moulds of a brachial valve. Despite different registration numbers, these are part and counterpart. Fig. 4 × 4.0 and fig. 5 × 7.0.

FIGS. 5 and 6. GSM 37589 and 37590. Exterior and interior moulds of a brachial valve. Holotype, figured Jones 1928, pl. 25, figs 2, 26. Despite different registration numbers, these are part and counterpart. × 6.0.

Aegiria grayi (Davidson)

Llandovery, Telychian, Hughley Shales, stream bank at Domas, near Harley, Shropshire, England. Grid Ref. SJ/5936 0062. Author's Collection.

FIG. 8. OUM C13973–5. External moulds (to left and right) and conjoined valves (centre). × 9.0.

Wenlock, Dudley Limestone, Staffordshire, England.

FIG. 9. B 780. Conjoined valves, lectotype. × 8.3. John Gray Collection.

FIG. 10. B 23205. Many conjoined valves. × 4.0. Caroline Birley Collection.

Llandovery, late Fronian or early Telychian, north bank of River Onny, Shropshire, England. Grid Ref. SO/4260 8532. Author's collection.

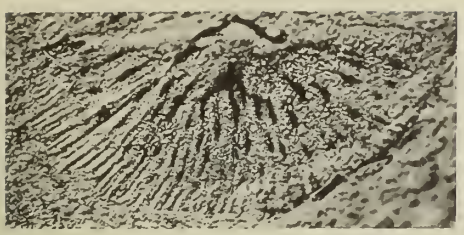
FIG. 11. OUM C12046. Pedicle internal mould. × 10.

FIG. 12. OUM C12051–2. Internal moulds of brachial valves. × 11.

Ludlow, Upper Leintwardinian, Chonetoidea Beds, Pont Shoni, Builth, Radnorshire, Wales. Grid Ref. SO/078 468. Author's collection.

FIG. 13. BB 32430. Pedicle internal mould. × 8.4.

FIG. 14. BB 32431. Brachial internal mould. × 13.



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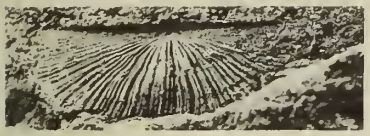

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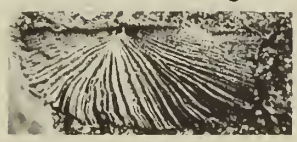

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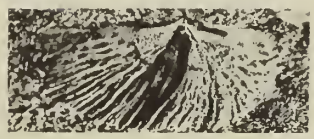

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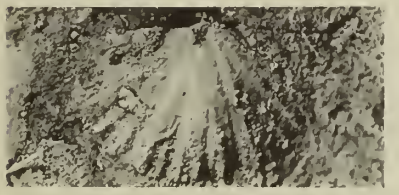

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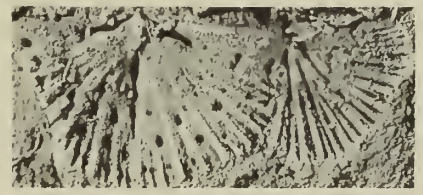

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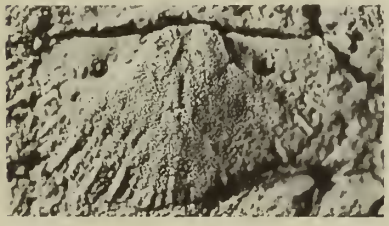

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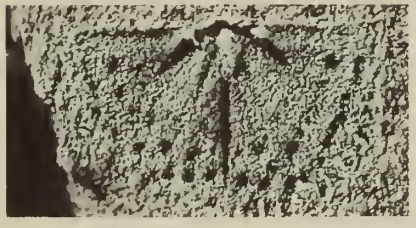

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